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Diet composition for three sciaenids caught off northeastern Brazil

Composición de la dieta de tres sciaenidos capturados en el nordeste de Brasil

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Resumen. *Larimus breviceps*, *Isopisthus parvipinnis* y *Paralonchurus brasiliensis* son las 3 especies de Sciaenidae más abundantes en la Reserva Extractiva Marina de Corumbau, en Bahia, nordeste de Brasil. Se analizaron los cambios ontogenéticos y estacionales en las dietas de estas especies. Estos cambios pueden reflejar las adaptaciones y mecanismos de coexistencia utilizados por estas especies. El muestreo se llevó a cabo entre diciembre 2007 y septiembre 2008 con arrastreros. Los peces y las gambas fueron los principales recursos consumidos por estas 3 especies. Para *L. breviceps* y *P. brasiliensis*, Sergestidae fue el alimento dominante (junto con poliquetos para el segundo), mientras que los peces fueron el elemento más importante para *I. parvipinnis*. Se observaron valores bajos de amplitud de nicho para todas las especies. El Índice de Similitud de Morisita indicó baja superposición entre las dietas de las 3 especies en la mayoría de las estaciones del año, a excepción de *L. breviceps* y *I. parvipinnis*, que mostraron valores superiores al 80% en todas las estaciones, excepto en verano. Aunque estas especies mostraron diferencias en la posición y orientación de su boca, esencialmente utilizan los mismos recursos. El hábito de alimentación carnívoro, principalmente carcinófago, prevaleció entre los Sciaenidae estudiados.

Palabras clave: Hábitos de alimentación, coexistencia, superposición de nicho, amplitud de nicho, nordeste de Brasil

Abstract. *Larimus breviceps*, *Isopisthus parvipinnis*, and *Paralonchurus brasiliensis* are the 3 most abundant species of Sciaenidae in the Marine Extractive Reserve of Corumbau in Bahia (northeastern Brazil). Ontogenetic and seasonal changes in the diet of these species were analyzed. These changes may reflect adaptations and coexistence mechanisms used by those species. Sampling took place between December 2007 and September 2008 with otter trawlers. Fishes and shrimps were the main resources consumed by these 3 species. For *L. breviceps* and *P. brasiliensis*, Sergestidae was the dominant food item (together with polychaetes for the latter) and fishes were the most important item for *I. parvipinnis*. Low values of niche breadth were observed for all species. The Morisita Similarity Index indicated a general pattern of low overlap between the diets of the three species analyzed in most of the seasons, with the exception of *L. breviceps* and *I. parvipinnis*, which showed values higher than 80% in all seasons, with the exception of summer. Although these species showed differences in the position and orientation of their mouth, they essentially use the same resources. The carnivorous feeding habit prevailed among the studied Sciaenidae, with predominance of the carcinophagous habit.

Key words: Feeding habits, coexistence, niche overlap, niche breadth, northeastern Brazil

INTRODUCTION

Species of the family Sciaenidae, commonly known as croakers, weakfishes, and drums, are widely distributed, and may be found in the Atlantic, Indian, and Pacific Oceans (Froese & Pauly 2016). Most of these species are often found in shallow waters of coastal regions, close to large rivers' mouths, over sandy or muddy bottom (Menezes & Figueiredo 1980), habitats that correspond to traditional Atlantic fishing grounds. This is one of the most abundant groups of demersal fishes found along the

Brazilian coast (Lowe-McConnell 1999), and it is one of the most important components of the demersal fish community in southern and southeastern Brazil (Bail & Branco 2003). In the northeast region, Sciaenidae also stands out due to the high number of species caught, according to a study carried out by Romero *et al.* (2008) in Ilhéus (state of Bahia). Although some species are commercially important, such as the whitemouth croaker (*Micropogonias furnieri*), most species of Sciaenidae

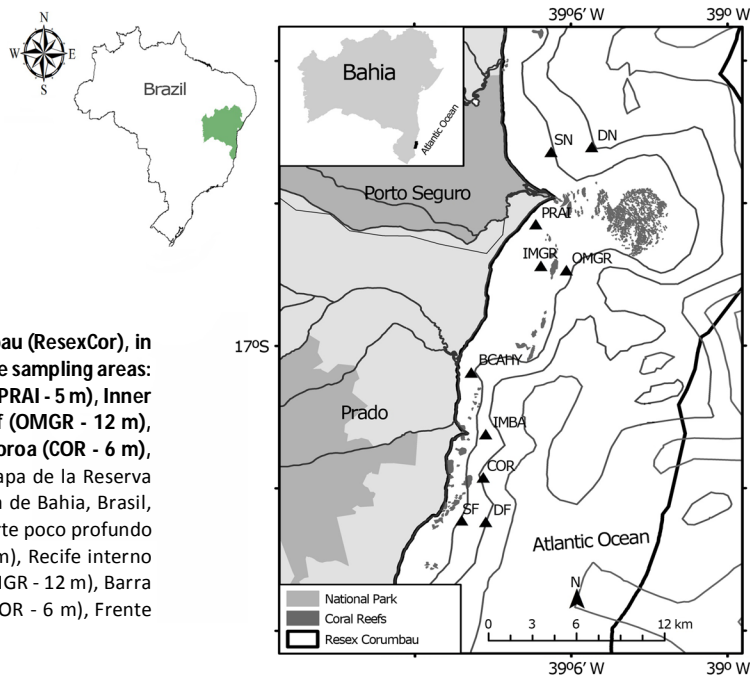


Figure 1. Map of the Marine Extractive Reserve of Corumbau (ResexCor), in the state of Bahia, Brazil, with black triangles indicating the sampling areas: Shallow north (SN - 5 m), Deep north (DN - 10 m), Prainha (PRAI - 5 m), Inner Mato Grosso Reef (IMGR - 7 m), Outer Mato Grosso Reef (OMGR - 12 m), Barra do Cahy (BCAHY - 6 m), Imbassuaba (IMBA - 6 m), Coroa (COR - 6 m), Shallow front (SF - 5 m), and Deep front (DF - 10 m) / Mapa de la Reserva Extractiva Marina de Corumbau (ResexCor), en la Provincia de Bahia, Brasil, con triángulos negros indicando las zonas de muestreo: Norte poco profundo (SN - 5 m), Norte profundo (DN - 10 m), Prainha (PRAI - 5 m), Recife interno Mato Grosso (IMGR - 7 m), Recife externo Mato Grosso (OMGR - 12 m), Barra do Cahy (BCAHY - 6 m), Imbassuaba (IMBA - 6 m), Coroa (COR - 6 m), Frente poco profundo (SF - 5 m), y Frente profundo (DF - 10 m)

are a major part of bycatch in shrimp trawling operations (Alverson *et al.* 1994) and small specimens are discarded.

The study of feeding habits is essential to understand the functional role of fishes in an ecosystem, even for species with no commercial interest (Muto *et al.* 2001). In addition to its importance in number and/or biomass for communities (Meyer & Smaller 1991), non-commercial species can be predators or competitors of commercially important species, and may interfere with their mortality rate (Muto *et al.* 2001). Thus, studies on the trophic structure address different aspects of the energy flow and relationships between predator and prey, and consumer and producer. These factors can explain coexistence mechanisms of some species and their contribution as members of the trophic web, in addition to provide a better interpretation of the community's structure (López-Peralta & Arcila 2002). Additionally, the diet composition is used to build trophic models (Rocha *et al.* 2007, Freire *et al.* 2008) and to enable the identification of factors affecting the distribution and abundance of the species investigated, including biological interactions, such as competition and predation (Deus & Petrere-Júnior 2003, Fonteles-Filho 2011).

One characteristic of competition is that resources are limited (Begon *et al.* 1996). Thus, to avoid competition, species share resources in different ways, which, according to Ross (1986), explains most of the coexistence mechanisms between closely related species. Moreover, the broad morphological variety

observed among species sharing habitats (different tooth types, mouth size and orientation, gill raker size and spacing, intestine size, etc.) reflects adaptations to make use of food items available (Zavala-Camin 1996, Fugi *et al.* 2001). If there is no sufficient morphological differentiation between two or more species, consumed resources may be similar, resulting in overlapping of niches and inter-specific competition may prevail (Begon *et al.* 1996).

In this context, the objective of this study was to analyze the diet of the three most abundant species of Sciaenidae (*Larimus breviceps*, *Isopisthus parvipinnis* and *Paralichthys brasiliensis*) occurring in the Marine Extractive Reserve of Corumbau, in the state of Bahia, and to test the hypothesis that diet overlapping is low among them considering their co-occurrence in high abundance and the difference in their mouth positioning. Even though the diet of these species have been analyzed in other regions (see *e.g.*, Soares 1989, Bessa *et al.* 2014, Muto *et al.* 2014), they were never studied in southern Bahia.

MATERIALS AND METHODS

STUDY AREA

The Marine Extractive Reserve of Corumbau (ResexCor) was established in September 21, 2000 with an area of about 895 km² (BRASIL 2000)¹ (Fig. 1). The reserve is located in the

¹BRASIL. 2000. Decreto N. 9036, September 21st 2000. Cria a Reserva Extrativista Marinha do Corumbau nos Municípios de Porto Seguro e Prado, Estado da Bahia, e dá outras providências. Diário Oficial [da] República Federativa do Brasil, Brasília, DF, N. 184, p.93, September 22nd 2000, Seção 1[21]. <http://www.planalto.gov.br/ccivil_03/dnn/2000/Dnn9036.htm>

extreme south of the state of Bahia, between the cities of Porto Seguro and Prado, comprising a fishing area between Ponta do Espelho, at Coruípe Beach (16°43'20"S - 39°07'11"W), and Barra do Rio das Ostras (17°13'29"S - 39°12'51"W). Artisanal fishing is allowed in this category of reserve. Its climate is tropical wet and its waters are dominated by the Brazil Current, responsible for high temperature and salinity throughout the year (Dutra *et al.* 2002)².

DATA COLLECTION

Four samplings were carried out from 2007 to 2008: spring (December 2007), summer (March 2008), fall (June 2008), and winter (September 2008). Specimens were collected by shrimp otter trawlers using a net with 30 mm mesh size in the net body and 26 mm in the 2 m long cod-end. Trawling was performed during the morning for an average of 30 min at a speed of 1.2 nautical miles h⁻¹. The fishing grounds were located between the villages of Corumbau, to the north of ResexCor, and Cumuruxatiba, to the south. The individual sites were (Fig. 1): Shallow north (SN - 5 m), Deep north (DN - 10 m), Prainha (PRAI - 5 m), Inner Mato Grosso Reef (IMGR - 7 m), Outer Mato Grosso Reef (OMGR - 12 m), Barra do Cahy (BCAHY - 6 m), Imbassuaba (IMBA - 6 m), Coroa (COR - 6 m), Shallow front (SF - 5 m), and Deep front (DF - 10 m).

The species of Sciaenidae caught were identified according to Menezes & Figueiredo (1980). The diet composition of *Larimus breviceps* Cuvier, 1830, *Isopisthus parvipinnis* (Cuvier, 1830) and *Paralanchurus brasiliensis* (Steindachner, 1875), the 3 most abundant species of Sciaenidae in the area, was studied. Fish specimens were weighed to the nearest gram and had their total length measured to the nearest mm. The mouth orientation of these species was observed (Fig. 2). Stomachs were removed, fixed in 10% formalin solution and then transferred to 70% ethanol for analysis of their food contents under stereoscopic microscope. The total number of specimens analyzed was based on sub-samples, selected for stomach content analysis, after excluding individuals whose stomachs were damaged. Gonads were later taken out for macroscopic identification of sex, according to Vazzoler (1996). Stomach contents were identified to the lowest possible taxonomic level (Ruppert & Barnes 1996). Dendrobranchiata shrimps were identified by Dr. Alexandre Almeida (Laboratory of Animal Histology, Universidade Estadual de Santa Cruz, Bahia). The category 'Others' represents unidentified animal organic matter.

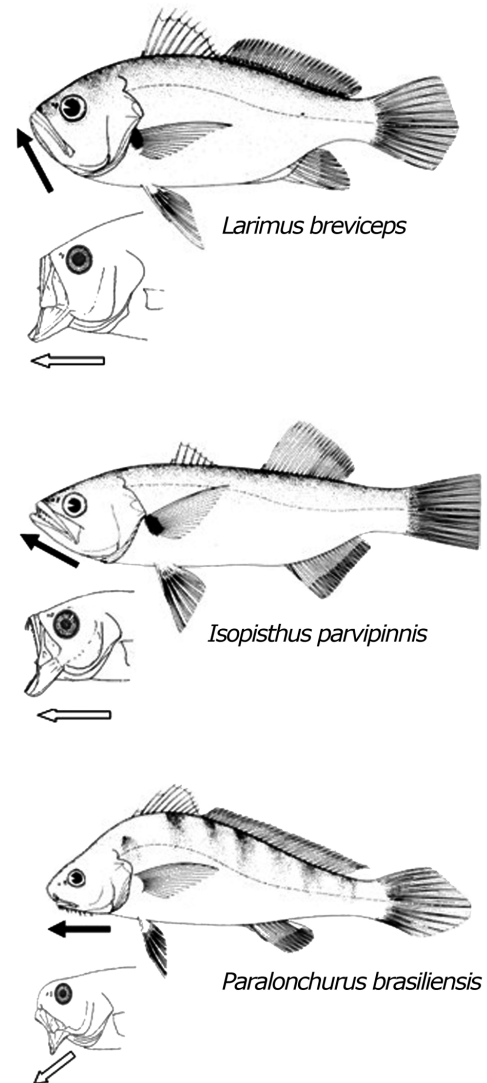


Figure 2. Sciaenidae species studied in the Marine Extractive Reserve of Corumbau. Black arrows indicate the mouth orientation when closed and white arrows, when opened. Source: Jucá-Chagas (1997) and Froese & Pauly (2016) (modified) / Especies de Sciaenidae estudiadas en la Reserva Extractiva Marina de Corumbau. Setas negras indican la orientación de la boca cuando cerrada y setas blancas, cuando abierta. Fuente: Jucá-Chagas (1997) y Froese & Pauly (2013) (modificado)

²Dutra GF, AZ Cordeiro, RV Carvalho & S Ortega. 2002. Reserva Extrativista Marinha do Corumbau. Plano de Manejo, Fase I, 15 pp.

DATA ANALYSIS

The diet was characterized based on the Frequency of Occurrence (FO, %), which indicates the proportion of the number of stomachs where a certain type of food item was found in relation to the total number of stomachs examined, and on the volumetric proportion (V, %), which measures the relationship between the volume of each type of food item and the total volume of all items found in the stomach (Hyslop 1980, Zavala-Camin 1996). FO and V were used to calculate the Food Index (IA_i, %):

$$\%IA_i = \frac{\%FO_i \times \%V_i}{\sum_i (\%FO_i \times \%V_i)} \times 100 \quad (1)$$

where: IA_i = food index; i = 1, 2, ... n; n = total number of types of food items; FO_i = frequency of occurrence of food item i in %; V_i = volume of food item i in relation to the volume of all items, in % (Kawakami & Vazzoler 1980). FO and IA_i were used to investigate ontogenetic and seasonal changes in the diet of the three species.

The degree of stomach fullness was visually estimated considering 4 categories: empty (0%), moderate (0% < X ≤ 25%), almost full (25% < X ≤ 75%) and full (>75%) (adapted from Muto *et al.* 2001).

The Levin's measure was used to analyze the niche of each species:

$$B = \frac{1}{\sum p_j^2} \quad (2)$$

where: B = Levin's measure of niche breadth; p_j = proportion of individuals using resource j or fraction of item j in the diet (Krebs 1989). It measures the uniformity of distribution of individuals among the types of resource. Thus, B is maximum when an equal number of individuals is recorded for each type of food resource, and minimal when all prey items correspond to only one type of resource (minimum niche breadth, maximum specialization). Thus, the value of B will be higher when more items are consumed in equal proportions.

The Morisita Index was used to verify the diet overlap between each pair of species analyzed:

$$CH_{jk} = \frac{2 \sum_i^n p_{ij} \cdot p_{ik}}{\sum_i^n p_{ij}^2 + \sum_i^n p_{ik}^2} \quad (3)$$

CH_{jk} = Simplified Morisita Index of diet overlap between

species j and k; p_{ij} = proportion of food category i in relation to the total number of items consumed by species j; p_{ik} = proportion of food category i in relation to the total number of items consumed by species k; n = total number of food categories (i = 1, 2, 3, ..., n) (Krebs 1989). Values higher than 0.5 indicate high diet overlap.

The Unweighted Pair Group Method (UPGMA) for cluster analysis and the Modified Morisita Similarity Coefficient were applied to compare the diet composition, using the software MVSP 3.1 (Multivariate Statistical Package).

RESULTS

FEEDING ECOLOGY

Larimus breviceps

A total of 498 stomachs of *L. breviceps* were analyzed, and 12 food categories were identified. Dendrobranchiata were identified using eyes and fragments of the carapace. These shrimps showed high IA_i in all seasons, with highest totals in the summer (Table 1). Two families of Dendrobranchiata were identified: Sergestidae and Penaeidae. Sergestidae was more frequently consumed throughout the year, except in the summer, with highest values of IA_i in the fall (26.2%) and winter (15.5%). Fishes were also present in diet of this species, with higher IA_i in the spring and fall. The high degree of digestion did not allow the identification of some specimens, which were grouped in the category 'unidentified fishes'. Among those that could be identified, individuals of the families Engraulidae and Sciaenidae were observed. Both families presented higher IA_i in the fall.

Empty stomachs accounted for only 5% of the total analyzed for this species in all seasons, with lower occurrence in the fall (Table 1). In the spring, about 52% of the stomachs analyzed were up to 25% filled with food; in the summer this percentage was higher.

Throughout the year, *L. breviceps* showed low values of niche breadth, especially in summer, when the diet of the species was composed mainly by Dendrobranchiata shrimps. The largest value was recorded in the fall (B = 3.29), when a lower dominance of shrimps and a small increase in fish consumption were observed (Table 1).

In two size classes for *L. breviceps*, Dendrobranchiata was the most important category, with IA_i of about 94% for individuals up to 10 cm long and 77% for individuals 10-20 cm long (Table 2). Only three individuals 20-30 cm long were found in the samples. Thus, this class was removed from the analysis.

Table 1. Seasonal variation of the food categories for *Larimus breviceps* in the Marine Extractive Reserve of Corumbau. Frequency of occurrence (%FO), volume (%V), Food Index (%IA_i), degree of stomach fullness (%), niche breadth (B), number of stomachs analyzed (N), and total length (TL, cm). *Non-identified animal organic matter due to the high degree of digestion and polychaete tubes / Variación estacional de las categorías tróficas de *Larimus breviceps* en la Reserva Extractiva Marina de Corumbau. Frecuencia de ocurrencia (%FO), volumen (%V), Índice Alimentario (%IA_i), amplitud de nicho (B), repleción estomacal (%), número de estómagos analizados (N), y longitud total (TL, cm). *Materia orgánica animal no identificada por la elevada digestión y tubos de poliquetos

Food Category	DEC/07 Spring			MAR/08 Summer			JUN/08 Fall			SEP/08 Winter		
	%FO	%V	%IA _i	%FO	%V	%IA _i	%FO	%V	%IA _i	%FO	%V	%IA _i
Unidentified Dendrobranchiata	71.8	53.5	83.9	62.9	75.0	89.6	78.7	41.2	68.5	69.2	56.0	83.0
Sergestidae	18.4	34.5	13.9	2.4	2.4	0.1	36.1	34.4	26.2	24.6	29.3	15.5
Penaeidae	3.1	2.1	0.1	2.4	3.9	0.2	5.7	3.3	0.4	4.6	2.6	0.3
Isopoda	3.7	0.3	0.0	0.0	0.0	0.0	2.5	0.2	0.0	1.5	0.6	0.0
Amphipoda	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Unidentified fish	16.6	3.9	1.4	8.1	4.0	0.6	18.9	9.8	3.9	1.5	0.5	0.0
Engraulidae	0.0	0.0	0.0	0.0	0.0	0.0	3.3	6.3	0.4	0.0	0.0	0.0
Sciaenidae	1.2	1.9	0.1	0.0	0.0	0.0	3.3	2.8	0.2	1.5	7.7	0.3
Cephalopoda (squid)	0.6	1.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Bivalvia	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Plant material	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Other*	8.0	3.6	1.0	33.9	14.7	9.0	9.0	1.9	0.0	16.9	3.3	1.0
Stomach fullness (%)												
Empty (0)		3.0			3.1			0.8			19.2	
Moderate (0<X≤25)		52.4			77.3			34.7			50.0	
Almost full (25<X≤75)		33.9			11.7			33.9			21.8	
Full (>75)		10.7			7.8			30.6			9.0	
B		2.44			1.70			3.29			2.46	
N		168			128			124			78	
TL (min-max)		6.1-22.0			8.7-15.3			3.8-18.8			6.5-48.9	

Table 2. Ontogenetic variation of food items found in the stomach content of species of Sciaenidae in the Marine Extractive Reserve of Corumbau, based on the Food Index (%IA_i). Total length class (cm): 1-10; 10-20; 20-30; number of stomachs analyzed (N). *Others: non-identified animal organic matter due to the high degree of digestion; in *I. parvipinnis* and *P. brasiliensis* includes plant material. DAOM= Digested animal organic matter / Variación ontogenética de ítems alimenticios encontrados en los contenidos estomacales de especies de Sciaenidae en la Reserva Extractiva Marina de Corumbau, basada en el Índice Alimentario (%IA_i). Clases de talla total (cm): 1-10; 10-20; 20-30; número de estómagos analizados (N). *Otros: materia orgánica animal no identificada por la elevada digestión; en *I. parvipinnis* y *P. brasiliensis* incluye material vegetal. DAOM = materia orgánica animal digerida

Food category	<i>Larimus breviceps</i>		<i>Isopisthus parvipinnis</i>			<i>Paralonchurus brasiliensis</i>		
	1-10	10-20	1-10	10-20	20-30	1-10	10-20	20-30
Unidentified Dendrobranchiata	94.4	77.1	91.1	52.6	41.7	59.8	59.3	63.0
Sergestidae	3.3	18.6	0.1	0.2	0.0	0.0	0.2	0.0
Penaeidae	0.1	0.3	2.4	0.4	7.4	0.0	0.0	0.0
Unidentified fish	0.8	2.0	4.7	28.9	1.6	0.1	0.1	0.0
Engraulidae	0.0	0.1	0.0	0.4	0.0	0.0	0.0	0.0
Sciaenidae	0.0	0.1	0.1	0.3	0.0	0.0	0.0	0.0
Clupeidae	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0
DAOM Polychaeta	0.0	0.0	0.0	0.0	0.0	13.9	27.3	5.3
Plant material	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0
Sediment	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.0
Others*	1.3	1.7	1.5	16.1	49.3	26.0	13.1	31.7
N	182	286	145	140	13	65	154	9

Isopisthus parvipinnis

Nine food categories were identified in 395 analyzed stomachs. The category Dendrobranchiata n.i. was important throughout the year, accounting for 67% of the IA_i in the spring and about 80% in the fall (Table 3). Similar to the diet of *L. breviceps*, Sergestidae and Penaeidae were found in the stomach contents. Fishes were the second most abundant food category in the diet of *I. parvipinnis*, showing the highest values of IA_i in the fall (15%) and winter (16%). In addition to the families Engraulidae and Sciaenidae, also ingested by *L. breviceps*, *I. parvipinnis* ingested clupeids, but with low IA_i values, mainly in the winter (2.3%).

Of the total of stomachs analyzed, only 10% were full, whereas most stomachs were classified as moderate (fullness degree: 0% < X ≤ 25%), especially in the summer (93.7%) (Table 3). In this season, due to the high degree of digestion of food consumed, only Dendrobranchiata shrimps were identified (IA_i = 41.1%). The lowest niche breadth was recorded in the summer (B = 2.00) and the largest in the winter (B = 5.17), when

fishes and shrimps (Sergestidae and Penaeidae) were consumed in similar proportions.

Dendrobranchiata shrimps dominated the diet of all size classes. Shrimps were largely consumed, mainly by individuals of up to 10 cm long, with an IA_i of around 91%. However, these percentages decreased among individuals 10-20 cm long, which ingested higher number of fishes (IA_i = 28.9%) (Table 2).

Paralonchurus brasiliensis

Nine food categories were identified in 242 analyzed stomachs. The highest IA_i values observed were represented by polychaetes in spring and fall and by Dendrobranchiata shrimps in summer and winter (Table 4). Among the shrimps that could be identified, Sergestidae were more important than Penaeidae. Other crustaceans, such as amphipods, were also identified in the diet of *P. brasiliensis*, but only in the winter. For this species, the category 'Others' includes polychaete tubes besides animal organic matter of unidentified origin.

Table 3. Seasonal variation of the food categories for *Isopisthus parvipinnis* in the Marine Extractive Reserve of Corumbau. Frequency of occurrence (%FO), volume (%V), Food Index (%IA_i), degree of stomach fullness (%), niche breadth (B), number of stomachs analyzed (N), and total length (TL, cm). * Non-identified animal organic matter due to the high degree of digestion / Variación estacional de las categorías tróficas de *Isopisthus parvipinnis* en la Reserva Extractiva Marina de Corumbau. Frecuencia de ocurrencia (%FO), volumen (%V), Índice Alimentario (%IA_i), amplitud de nicho (B), repleción estomacal (%), número de estómagos analizados (N), y talla total (TL, cm). *Materia orgánica animal no identificada por la elevada digestión

Food category	DEC/07 Spring			MAR/08 Summer			JUN/08 Fall			SEP/08 Winter		
	%FO	%V	%IA _i	%FO	%V	%IA _i	%FO	%V	%IA _i	%FO	%V	%IA _i
Unidentified Dendrobranchiata	52.0	43.6	67.0	40.0	51.2	41.1	62.1	47.1	80.3	46.1	22.6	51.7
Sergestidae	0.0	0.0	0.0	0.0	0.0	0.0	1.2	0.7	0.0	7.9	4.6	1.8
Penaeidae	0.0	0.0	0.0	0.0	0.0	0.0	7.7	9.7	2.0	7.9	15.9	6.2
Unidentified fish	12.0	20.1	7.0	0.0	0.0	0.0	20.1	28.1	15.5	13.2	25.6	16.8
Engraulidae	2.0	10.0	5.0	0.0	0.0	0.0	0.6	0.8	0.0	0.0	0.0	0.0
Sciaenidae	0.0	0.0	0.0	0.0	0.0	0.0	2.4	9.9	0.6	0.0	0.0	0.0
Clupeidae	2.0	8.0	0.0	0.0	0.0	0.0	0.6	0.8	0.0	2.6	17.2	2.3
Plant material	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.1	0.0	0.0	0.0	0.0
Others	38.0	18.2	20.0	60.0	48.8	59.0	14.8	3.5	1.0	30.3	14.1	21.0
Stomach fullness (%)												
Empty (0)	24			0			27.8			20		
Moderate (0 < X ≤ 25)	62			93.7			42.3			55.8		
Almost full (25 < X ≤ 75)	12			6.2			17.9			10.5		
Full (>75)	2			0			12			13.7		
B	3.57			2.00			3.11			5.17		
N	50			16			234			95		
TL (min-max)	7.4-28.4			11.0-22.5			3.9-23.5			3.6-22.2		

Table 4. Seasonal variation of the food categories for *Paralonchurus brasiliensis* in the Marine Extractive Reserve of Corumbau. Frequency of occurrence (%FO), volume (%V), Food Index (%IA_i), degree of stomach fullness (%), niche breadth (B), number of stomachs analyzed (N), and total length (TL, cm). * Non-identified animal organic matter due to the high degree of digestion / Variación estacional de las categorías tróficas de *Paralonchurus brasiliensis* en la Reserva Extractiva Marina de Corumbau. Frecuencia de ocurrencia (%FO), volumen (%V), Índice Alimentario (%IA_i), amplitud de nicho (B), repleción estomacal (%), número de estómagos analizados (N), y talla total (TL, cm). *Materia orgánica animal no identificada por la elevada digestión

Food category	DEC/07 Spring			MAR/08 Summer			JUN/08 Fall			SEP/08 Winter		
	%FO	%V	%IA _i	%FO	%V	%IA _i	%FO	%V	%IA _i	%FO	%V	%IA _i
Unidentified Dendrobranchiata	61.5	10.4	24.4	27.3	36.2	27.1	60.7	24.9	28.3	58.6	53.0	75.6
Sergestidae	7.7	4.6	1.2	0.0	0.0	0.0	14.3	8.2	2.5	1.7	0.5	0.0
Penaeidae	3.1	2.8	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Amphipoda	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.7	0.1	0.0
Unidentified fish	1.5	4.6	0.3	2.6	1.5	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Polychaeta	24.6	31.4	29.3	13.0	19.7	7.0	57.1	64.5	69.0	31.0	23.2	17.5
Sediment	3.1	2.8	0.3	0.0	0.0	0.0	0.0	0.0	0.0	5.2	2.2	0.3
Plant material	0.0	0.0	0.0	2.6	2.8	0.2	10.7	0.1	0.2	0.0	0.0	0.0
Others*	24.6	48.7	45.0	59.7	39.9	66.0	10.7	1.5	0.0	19.0	20.1	6.0
Stomach fullness (%)												
Empty (0)		4.4			9.3			12.9			0	
Moderate (0<X≤25)		55.9			73.3			45.16			66.7	
Almost full (25<X≤75)		32.4			14.0			22.58			22.8	
Full (>75)		7.4			3.5			19.35			10.5	
B		2.86			3.03			2.06			2.78	
N		68			86			31			57	
TL (min-max)		5.7-21.7			5.8-22.0			4.7-19.4			4.6-23.5	

About 63% of stomachs examined for this species were up to 25% filled with food and only 6 were empty. Moderate stomachs were more frequent in the summer, when only 3.5% of the stomachs were full (Table 4). The widest niche breadth for *P. brasiliensis* was observed in spring and summer, when the dominance of polychaetes and Dendrobranchiata shrimps was lower. On the other hand, the lowest niche breadth was recorded in the fall, when high values of IA_i were observed for polychaetes and Dendrobranchiata.

Dendrobranchiata was equally important in all size classes identified for *P. brasiliensis*, followed by polychaetes, which were particularly important to individuals 10-20 cm long (Table 2).

DIET OVERLAP

The Morisita Similarity Index exhibited a general pattern of low overlap between the diets of the three species analyzed (Fig. 3). In spring, summer and fall, the diet overlap between *P. brasiliensis* and *L. breviceps* was low ($CH_{jk} < 0.50$), reflecting low values of Dendrobranchiata shrimps observed in the diet of *P. brasiliensis*, in contrast to values twice or three times higher for *L. breviceps*. A similar pattern was observed for *P. brasiliensis* and *I. parvipinnis*, with low diet overlap specially in summer ($CH_{jk} = 0.22$). In the fall, *P. brasiliensis* showed low similarity with the diet of other species, due to a higher abundance of polychaetes in its diet.

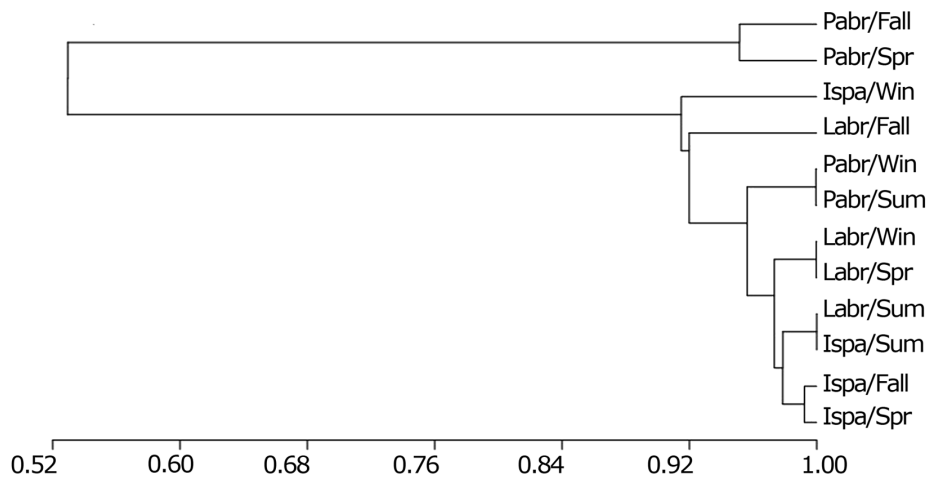


Figure 3. Seasonal feeding similarity between the species of Sciaenidae according to the Modified Morisita Similarity Coefficient (Labr: *Larimus breviceps*; Ispa: *Isopisthus parvipinnis*; Pabr: *Paralanchurus brasiliensis*; Spr: spring; Sum: summer; Fall: fall; Win: winter) / Similitud alimentaria estacional entre especies de Sciaenidae de acuerdo con el Coeficiente de Similitud Modificado de Morisita (Labr: *Larimus breviceps*; Ispa: *Isopisthus parvipinnis*; Pabr: *Paralanchurus brasiliensis*; Spr: primavera; Sum: verano; Fall: otoño; Win: invierno)

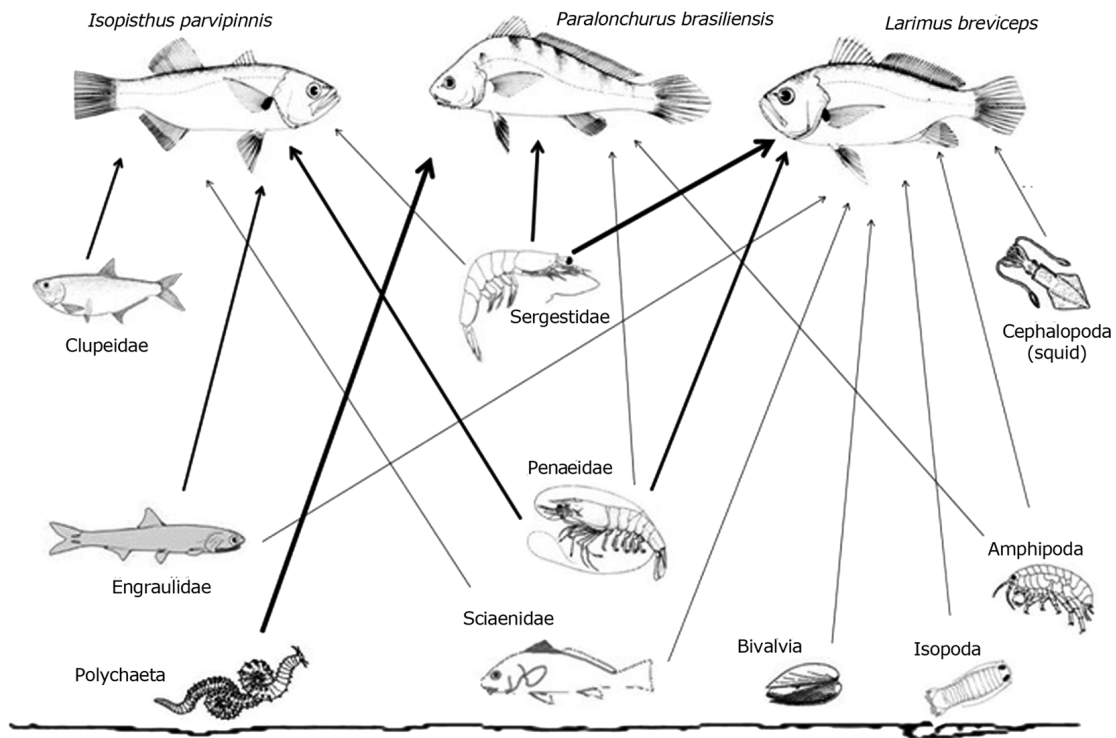


Figure 4. Trophic interactions among the three most abundant sciaenids in the ResexCor based on frequency of occurrence (%FO) of food items found in the stomach content. The width of the arrows is proportional to the FO of each item in the diet of each species as defined / Interacciones tróficas entre las tres especies abundantes de Sciaenidae en la ResexCor basado en la frecuencia de ocurrencia (%FO) de ítems encontrados en el contenido estomacal. La largura de las setas es proporcional a FO de cada ítem en la dieta de cada especie como definido

Very high indexes of overlap were observed only in the winter between *P. brasiliensis* and *L. breviceps* ($CH_{jk} = 0.95$) and between *P. brasiliensis* and *I. parvipinnis* ($CH_{jk} = 0.83$), due to the high abundance of Dendrobranchiata shrimps in the diet of the three species (Tables 1 and 4).

On the other hand, *L. breviceps* and *I. parvipinnis* showed diet overlap higher than 80% in all seasons, except in summer ($CH_{jk} = 0.56$). During this season, the IAI for Dendrobranchiata shrimps was about twice as higher as for *L. breviceps*. However, besides the abundance of Dendrobranchiata in both diets, Sergestidae was more important to *L. breviceps* mainly in the fall (26.2%), while Penaeidae showed higher IAI in the diet of *I. parvipinnis*.

For the 3 species of Sciaenidae, the trophic relations studied in the ResexCor seem to indicate low food overlap between *P. brasiliensis* and each of the other 2 species (except during winter), and high diet overlap between *L. breviceps* and *I. parvipinnis*. This is represented in Figure 4 where the thickness of the arrow is proportional to the frequency of occurrence (%FO).

DISCUSSION

Morphological characteristics such as mouth orientation, shape, and size are related to the feeding habit of a species, and indicate how fishes locate and feed on its prey (Zavala-Camin 1996, Karpouzi & Stergiou 2003). In general, the overall mouth shape is similar among fish species but its detailed structure presents a wide variation from one group to another, allowing some species to feed upon a large variety of resources. However, the nature of the ingested food does not depend only on the morphological characteristics of the mouth, but also on the composition and availability of the resources in the environment (Berg 1979, Gerking 1994).

According to the Optimal Foraging Theory, species are capable of taking advantage of the abundance of a certain resource. Thus, the most abundant resource will usually be the most consumed by individuals (Gerking 1994, Hughes 1997). This might occur due to the absence, low abundance, or difficulty to capture the food of preference, leading the species to exploit other resources available in higher abundance than preferred prey. This is called trophic adaptability, which is responsible for changes in food habits in response to daily or seasonal variation in food availability (Gerking 1994, Lowe-McConnell 1999).

The importance of polychaetes in the diet of *P. brasiliensis* in the ResexCor was similar to that observed off southern Paraná, with FO exceeding 40% (Robert *et al.* 2007) and around 69% in the coast of the State of São Paulo (Jucá-Chagas

1997, Soares & Vazzoler 2001). However, these authors did not observe the same importance that shrimps had in our study area. The importance of polychaetes in the diet of sciaenids was also reported by Bertrán *et al.* (2013) for *Micropogonias furnieri* in Chile. Additionally, Robert *et al.* (2007) and Soares & Vazzoler (2001) observed the presence of fishes in the diet of *P. brasiliensis*, a food category of minor importance for this species in the ResexCor (0.8%).

The consumption of pelagic shrimps (Sergestidae) by *P. brasiliensis* in the study area was unexpected due to the mouth orientation of this species and its common benthivorous feeding habits. Gerking (1994) considers that, although the trophic adaptability is limited by mouth morphology, feeding behavior, and digestion capacity, it is not possible to predict the responses of consumers due to changes in the abundance of their prey. In this study, no information on the abundance of the prey was obtained and the limited sampling period did not allow for the assessment of possible changes in diet composition associated with a decrease in the abundance of preferred prey. Moreover, benthivorous predators have more diverse feeding habits than any other group. Even fishes that have extreme morphological specializations in their digestive tract will be able to use a variety of food categories according to their availability in the habitat at certain periods (Lowe-McConnell 1999). Therefore, by taking advantage of a food source that is not common in its diet, *P. brasiliensis* may be considered as an opportunistic species, able to catch and eat other less preferred prey whenever its preferred prey is overexploited or in low abundance (Gerking 1994). Thus, these possible supply fluctuations, in addition to the limited opening of its mouth proportional to the size of the ingested Sergestidae, may have contributed to the observed change in the diet of *P. brasiliensis*.

According to Zavala-Camin (1996), the consumption of solid food is usually a cyclic activity comprising ingestion, digestion, and rest. The latter corresponds to a period when the stomach remains empty. Although Soares & Vazzoler (2001) have not found strong evidence of a daily feeding pattern for *P. brasiliensis*, they observed a larger consumption of food items in the afternoon. A similar pattern was observed by these authors for *L. breviceps*, whose major consumption was registered at dusk and at night, and for *I. parvipinnis*, which fed mainly in the afternoon, with some feeding activity at night. In this study, samples were collected only in the morning, leading to the capture of individuals with prey in advanced digestion stages. Therefore, the time of the capture is a factor that may cause quantitative changes in diet, in addition to factors such as the digestibility of the item. This might contribute to an overestimate of how many items were actually ingested, as carapace and pereopods of crustaceans can stay longer in the stomach than

polychaetes, which have soft and easily digestible body (Fonteles-Filho 2011).

According to Lowe-McConnell (1999), *L. breviceps* preys upon pelagic shrimps (Sergestidae), a feeding habit facilitated by their oblique, tilted up mouth. Studying the morphological aspects related to feeding, such as mouth orientation and shape and the arrangement of teeth, Jucá-Chagas (1997) found that shrimps and fishes are the most consumed category by various sciaenids off the state of São Paulo. Similarly to the results found in the ResexCor, Sergestidae shrimps were the most important food category in the diet of *L. breviceps* and *I. parvipinnis*. Dendrobranchiata and fishes were also the most important food items in the diet of *I. parvipinnis* off Ilhéus, in the state of Bahia (Romero *et al.* 2008). For *L. breviceps*, as for the other studied species, the mouth orientation was in accordance with the position occupied by its prey types available in the environment. When open, the mouth orientation of *L. breviceps* and *I. parvipinnis* is terminal (Fig. 2), a position adequate to capture pelagic items. On the other hand, the mouth of *P. brasiliensis* is sub-terminal (Fig. 2), properly fitted for catching benthic organisms such as polychaetes.

Analyzing the diet of juveniles of *L. breviceps* in Itaparica Island (Bahia), Moraes *et al.* (2004) observed Dendrobranchiata as one of the most frequent food categories, especially in summer. These results are similar to those found in the ResexCor, where this category was more frequent in spring and summer. In the study area, Cephalopoda, Isopoda, Bivalvia, and Amphipoda were considered occasional food resources, according to the definitions given by Fonteles-Filho (2011). The same result was found off the State of São Paulo and in Itaparica, in the state of Bahia (Jucá-Chagas 1997, Moraes *et al.* 2004).

Cannibalism in the diet of *L. breviceps* in the ResexCor was registered. Fishes were identified only to the family level due to the high degree of digestion of the food items. However, the oblique mouth and other morphological characteristics of these items are typical of *L. breviceps*, which indicates the presence of co-specific individuals in the stomach contents in the study area. Cannibalism was also reported in the diet of *L. breviceps* (Moraes *et al.* 2001, 2004) and *Macrodon ancylodon* (Figueiredo *et al.* 2014). According to Smith & Reay (1991), cannibalism may be considered as a type of predation with potential to regulate population density, being especially observed in piscivorous species or those exhibiting high levels of parental care. Smith & Reay (1991) list 35 families of marine and freshwater fishes in which cannibalism was recorded; however, Sciaenidae was not cited.

The ingestion of shrimps and fishes was observed in all 3 sciaenids analyzed here. However, minor differences in the diet should allow for more efficient exploitation of food resources, benefitting several species (Gerking 1994, Lowe-McConnell 1999). Some differentiation was observed for *L. breviceps* due to its higher efficiency to capture Sergestidae, which allows for higher consumption of this group in relation to other groups. *L. breviceps* is one of the sciaenids with the highest values of mouth height and width (Jucá-Chagas 1997), allowing it to capture a high number of Sergestidae during the feeding activity.

The species' niche breadth measures its level of specialization related to the use of local resources (Colwell & Futuyma 1971). Specialist species feed upon one or two food sources and will have a lower value of niche breadth than generalist species, which feed on many food categories (Colwell & Futuyma 1971, Gerking 1994). The high importance of shrimps and fishes in the diet of the three species analyzed in the ResexCor indicates that they exploit essentially the same resources, with a minor degree of differentiation, even though there is evident difference in the orientation of their mouth, accepting the initial hypothesis of low diet overlap. This could be related to the high local abundance of Dendrobranchiata shrimps in the study area. Muto *et al.* (2014) also categorized these 3 species in different trophic groups due to differences in the main ingested prey. However, more studies will be necessary on the diet of these species, with a more detailed taxonomic analysis of the food items (not possible here due to the high degree of digestion of stomach contents) and a more representative sampling scheme to further explore how food sharing takes place among these three locally abundant sciaenids.

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