

Do closely related species share of feeding niche along growth? Diets of three sympatric species of the mojarras (Actinopterygii: Gerreidae) in a tropical bay in southeastern Brazil

R. M. Vasconcellos · R. S. Gomes-Gonçalves · J. N. S. Santos · A. G. Cruz Filho · F. G. Araújo

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Abstract Understanding the trophic relationships among closely related species is a way to obtain subsidies for their management and conservation of their habitats. The diets of three co-occurring abundant fish species of the Gerreidae family (*Diapterus rhombeus*, *Eucinostomus argenteus* and *Eucinostomus gula*) in a tropical bay were described. The tested hypothesis was that the three sympatric species present shifts in their use of resource during the ontogenetic development to facilitate their coexistence. Size groups for each species

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R. M. Vasconcellos · R. S. Gomes-Gonçalves ·

F. G. Araújo (🖂)

Laboratório de Ecologia de Peixes, Universidade Federal Rural do Rio de Janeiro, BR 465, km 7, Seropédica, RJ CEP 23890-000, Brazil

e-mail: gersonufrrj@gmail.com

R. M. Vasconcellos

Instituto Federal de Educação, Ciência e Tecnologia de Mato Grosso do Sul (IFMS), Campus Ponta Porã, BR 463, Km 14, Sanga Puitã, Caixa Postal 287, Ponta Porã, MS, Brazil

J. N. S. Santos

Instituto Federal do Norte de Minas Gerais (IFNMG), Campus Almenara, Rodovia BR 367, Km 07, s/n – Zona Rural, Almenara, MG CEP 39900-000, Brazil

A. G. Cruz Filho

Laboratório de Ecologia de Ecossistemas Aquáticos, Fundação Instituto de Pesca do Estado do Rio de Janeiro (FIPERJ), Estação Experimental de Guaratiba, Avenida das Américas, 31501, Guaratiba, Rio de Janeiro, RJ CEP 23032-050, Brazil

were categorized according to breakpoints in the morphological structures determined by piecewise regression models. Significant overlapping in diets was found for all size classes of D. rhombeus but not for size classes of the Eucinostomus genus. Furthermore, different size classes of D. rhombeus did not overlap diet with size classes of the Eucinostomus genus. The specialization in feeding niches corresponding to growth seems to bring benefits for this group of fish rather than a generalist feeding strategy. The hypothesis of the available resources partitioning was accepted only between the two genera (Diapterus and Eucinostomus), and among size classes of the Eucinostomus genus that seemed to follow the principle of limiting similarity. However, different size classes of D. rhombeus exhibited strong evidence of an intraspecific overlapping of the trophic niche. It seems that different processes related to use of the trophic niche dimension are structuring these closely related fish species.

Keywords Estuarine · Fish · Trophic niche · Intraspecific partitioning · Ecology

Introduction

The description of the fish feeding habits and their changes allows understanding functions developed by the species within the ecosystems (Florin and Lavados 2010; Barrett et al. 2016), being also an important indicator of the trophic relationships among the species (Blaber 1997; Cruz-Escalona et al. 2000; Matich et al.

2017). Although knowledge of the prey selection among species may be indicative of the degree of organization of animal communities, studies on these issues are limited (Carrassón and Cartes 2002; Sedio et al. 2012). Understanding these processes is fundamental for the management of living resources and conservation of their habitats.

The majority of marine fish species are planktivorous at the onset of exogenous nutrition. Improvements in vision, development of fins and associated improvements in swimming performance, increases in gape size and development of the alimentary tract during ontogeny often lead to shifts in diet composition (Nunn et al. 2012). Feeding diversity generally is high during the early development. In this period, there is great importance of species-specific dietary traits. The use of resources is determined by differences in the size of the morphological apparatus used in the feeding process, modes of feeding, swimming ability, habitat use and type and prey size, among other factors (Hourston et al. 2004). Morphological changes enhance swimming ability (Webb 1984) and resources use (Gatz Jr. 1979), thus influencing the growth and survival of young fish (Werner and Gilliam 1984).

Sympatric species with similar anatomic configuration have a strong competitive potential (Wootton 1990). For these species, ecological variations is expected in the use of available niches and/or partitioning of the available resources to enable their coexistence (Herder and Freyhof 2006; Sandlund et al. 2010). The partitioning of resources by coexisting species can be influenced by the ontogenetic process (Pessanha and Araújo 2014). Species that share morphological characteristics tend to have ecological similarities and are good target organisms to study resource-use strategies (Bonato and Fialho 2014). A large number of studies have shown that each population appears to be composed of ecologically heterogeneous individuals, each of which uses only a subset of the population's overall resource base (Bolnick et al. 2003). Individuals may mitigate the effects of inter-intraspecific competition if they use alternative resources not used by conspecific competitors (Schoener 1971; Svanbäck and Bolnick 2007). One of the most important strategies for resource partitioning among closely related species are changes along the ontogenetic dimension.

Species of the Gerreidae family are among the most common fish species inhabiting nearshore protected tropical waters such as sandy beaches in bays and estuarine areas (Pessanha and Araújo 2012; Franco et al. 2012; Ramos et al. 2014). Some studies on their distribution patterns and feeding ecology attempted to explain their coexistence in high abundances in coastal areas (Pessanha and Araújo 2014; Ramos et al. 2014). Understanding how these species explore different feeding resources and their strategies of resource uses along the ontogenetic development provide a good opportunity to detect the mechanisms for their coexistence. Thus, partitioning in the use of the available resources during the ontogenetic development may be a key strategy to species coexistence in estuarine areas. Ramos et al. (2014) found shifts in diet of Gerreidae fishes during their ontogenetic development in the Goiana estuary in Northeast Brazil, and reported that such shifts frequently coincided with changes in trophic niche and habitat use during growth, whereas seasonal changes had minor importance and corresponded to shifts in the proportions of prey. In the Sepetiba Bay, a coastal area in southeastern Brazil, the gerreids Diapterus rhombeus (Cuvier, 1829), Eucinostomus argenteus (Baird & Girard, 1855) and Eucinostomus gula (Quoy and Gaimard, 1824) are sympatric fish species with significant contribution to both the total number of individuals and biomass (Araújo et al. 2002, 2016b).

The aim of this study was to evaluate inter- and intraspecific changes in the diets of these three common fish species (*D. rhombeus*, *E. argenteus* and *E. gula*) in Sepetiba Bay and to assess whether these fish species can coexist successfully as a result of differences in dietary preference. We investigated changes in the diets of the three species during the ontogenetic development to assess indications of inter- and intraspecific partitioning of the feeding resources among different size groups. The tested hypothesis was that the three sympatric species are partitioning the feeding resources correlating with their growth, thus following the principle of limiting similarity.

Materials and methods

Study area

Sepetiba Bay (22°549′–23°049′S; 43°349′–44°109′W) (Fig. 1) is located in Rio de Janeiro State, southeastern Brazil, and has an area of 450 km², which encompasses a wide range of habitats, including mangroves, sandbanks and small estuarine areas (Fiszman et al. 1984;



Leal Neto et al. 2006). The mean depth is ca. 8 m. The waters are rich in organic nutrients from continental drainage, and the bottom is predominantly muddy. This microtidal system has tides ranging from 0.5 to 1.5 m in height. The average salinity is 30 and the mean temperature ranges from 20 to 27 °C. Small rivers and stream drain into the bay, contributing to decreases in the salinity and increases in the turbidity in the inner bay areas. The bay supports a rich and diversified fish fauna and is used as rearing grounds for several coastal fish species (Santos and Araújo 1997; Guedes et al. 2004; Guedes and Araújo 2008; Pessanha and Araújo 2014). In the last decade, this coastal system has suffered growing environmental degradation due to increases in industrial and municipal effluents brought into the bay by rivers and channels from the outskirts of the city of Rio de Janeiro (Leal Neto et al. 2006; Araújo et al. 2016b).

Sampling procedure

Fish were collected by beach seine (15 beach seines hauls) and by bottom trawling (15 trawls hauls) in the Sepetiba Bay in June 2009. All samples were collected during the day in the winter (dry season), when environmental conditions are more stable because of the comparatively lesser influence from heavy rains that carry into the bay organic loads or leaking pollutants. The beach seine net (12 m long \times 2.5 m height; 12 mm mesh) has a pocket of 5 mm mesh size in its rear portion. The net was set parallel to the shoreline in waters <1.5 m deep and then hauled straight to the shore. The swapped area was taken to be the distance the net was laid offshore (30 m) multiplied by the mean width of the haul (10 m), resulting in an effective fishing area of

approximately 300 m². The bottom trawling had an 8m headline, 11-m ground rope, 25-mm stretched mesh, and 12-mm mesh cod-end liner. Tows were against the current and covered an area of approximately 6000 m². The bottom depth in the trawled areas trawled ranged from 3 to 25 m.

Immediately after collection, all individuals were anaesthetized in benzocaine hydrochloride (50 mg l^{-1}) and then fixed in a 10% formaldehyde-seawater solution. After 48 h, the specimens were transferred to 70% ethanol. All individuals were identified to the species level, and the total length of each fish was measured (TL, in millimeters). The stomachs were removed, and each food item was identified to the lowest taxonomic level under a stereomicroscope. The food item was counted, and weighed to the nearest 0.001 g. A food item that weighed less than the accuracy of the balance was considered to have the minimum value of 0.001 g. Polychaeta fragments were counted considering the number of individuals heads, and the pooled fragments were weighted. As the number of Algae was not precisely counted, we considered only the total weight of the Algae fragments. Individual fish covering a wide range of sizes were selected for dissection. Empty stomachs or those with unidentifiable contents were excluded from the analyses.

Morphological measurements and size class assignments

From randomly selected, non-distorted and nondamaged individuals, a total of 22 external morphometric characteristics (Fig. 1) potentially associated with swimming ability and resource use were measured to the nearest 0.1 mm (Ponton and Mérigoux 2000; Sarpédonti et al. 2000). The morphological measurements were taken from digital images of lateral view (300 dpi) using the software ImageJ 1.3 (Abramoff et al. 2004). The dorsal morphological measurements were taken with a digital caliper precision 0.1 mm.

These characters were (Fig. 2): (1) the distance between the tip of the head and the posterior margin of the caudal fin (total length, TL); (2) the distance between the tip of the head and the posterior margin of the operculum (head length, HL); (3) the distance between the tip of the head and the anterior margin of the pectoral fin (head to pectoral fin, HPf); (4) the distance between the tip of the head and the anterior margin of the pelvic fin (head to pelvic fin, HPef); (5) the distance between the tip of the head and the anterior margin of the anal fin (head to anal fin, HAf); (6) the distance between the tip of the head and the anterior margin of the dorsal fin (head to dorsal fin, HDf); (7) the vertical distance from the anterior margin of the dorsal fin to the ventral margin of the body (body depth, BD); (8) the maximal height of the head (head height, HH); (9) the horizontal eye diameter (eye diameter, ED); (10) the pectoral fin length (pectoral length, PL); (11) the vertical distance from the dorsal margin to the ventral margin of the pectoral fin (pectoral height, PH); (12) maximum caudal peduncle depth (peduncle depth, PD); (13) the maximum vertical distance from the dorsal margin to the ventral margin of the caudal fin (caudal depth, CD); (14) the distance between the base to the tip of the caudal fin (caudal length, CL); (15) maximum body width (body width, BW); (16) maximum caudal peduncle width (peduncle width, PW); (17) maximum head width (head width, HW); (18) the distance between the two margins of the mouth fully open (mouth width, MW); (19) the distance between the lips of the lower and the upper maxilla with the mouth fully open (mouth height, MH); (20) the distance between the tip of the head and the distal part of the upper maxillary bone (upper maxilla, UM); (21) the distance between the tip of the head and the distal part of the low maxillary bone (lower maxilla, LM); and (22) the distance between the tip of the head and the anus (head to anus, HA).

The breakpoint method was used to separate fish size classes. This method was proposed by Kovač et al. (1999) and considers abrupt transitions of morphological features in relation to the total length. The method is designed to detect the inflection (turning point) between two intervals of isometric growth of a given character; each of these intervals presents a different isometry in the relation between the morphological characteristic and the body length. Thus, the size at which there are great numbers of breakpoints in morphometric structures should be assigned as a mark to establish size class limits. These inflections can be detected by pairwise linear regression models. Linear piecewise (split) regression models were fitted to the 21 morphometric characteristics against the TL. It was checked that the residuals



Fig. 2 A representative Gerreidae species, with indication of twenty-two morphological variables: \mathbf{a} lateral view; \mathbf{b} dorsal view; \mathbf{c} front view. Codes for the measurements in "Morphological measurement and size classes' assignment" sub-section

of the simple linear or split linear regressions did not present systematic patterns when plotted against the TL (Wilkinson et al. 1996) and then they were used for sizeindependent comparisons of the morphometric characters for each species (Reist 1985). Then, the breakpoint, expressed as total length, and two simple linear regressions were calculated for the data anterior and posterior to the breakpoint.

The mouth gape area (MA) and cross-sectional area of prey (PA) were estimated following the models proposed by Ward-Campbell et al. (2005), where, the mouth area was calculated assuming an elliptical shape: MA = $\pi \frac{1}{2}$ MH * $\frac{1}{2}$ MW, where MH, is Mouth Height and MW, is Mouth Width. The cross-sectional area of prey (PA) was estimated from the prey width and assuming the prey have a circular shape.

Data analyses

The food composition was expressed for each food item as a percentage of the Index of Relative Importance (IRI) developed by Pinkas et al. (1971), which describes the relative contribution of food items to the diet in terms of the frequency of occurrence (%FO), numerical percentage (%N) and mass (%M) (Hyslop 1980): IRI = (%N + %M) × %FO. The index for each feeding item was expressed as a percentage of the sum of all IRI scores: %IRI = (IRI / \sum IRI) × 100.

The prey weight data obtained for the food items were used to calculate the Levin's niche breadth (Krebs 1989): $B = 1 / \sum p_i^2$, where p_i , is the relative proportion of the item i in relation to the total items of the sample. Then, the standardized niche breadth, was calculated as $B_A = (B - 1) / (n - 1)$, where B is the niche breadth, and n, is total number of items. B_A ranges from 0 to 1, and values close to 1 indicate that a large number of food items are evenly distributed, whereas values closer to 0 indicate a few food items in an unevenly proportion are consumed.

The simplified Morisita overlap index (Krebs 1989) was used to assess the feeding niche overlap among species and size classes, as follow: $C_{ik} = 2 \sum_j P_{ij}P_{kj} / \sum_j P_{ij}^2 + \sum_j P_{kj}^2$, where C_{ik} is the simplified Morisita overlap index between species i and k, P_{ij} and P_{kj} are the proportion of the predators i and k with the prey j in the stomach. The simplified Morisita index was calculated based on the mass data for the food items. This index ranges from 0 to 1, with higher values indicating dietary overlap; although there were no critical levels with

which overlap values could be compared, Labropoulou and Eleftheriou (1997) suggested that values >0.6 should be considered as biologically significant.

The trophic strategy was assessed with the Costello graphical method (Costello 1990), modified by Amundsen et al. (1996). The food items were expressed as the percent composition of prey-specific mass (%M) in fish that contained a specific food item and the percentage frequency of occurrence (%FO). The %FO was plotted against the %M, and then interpreted with respect to its position on the graph.

Statistical analyses

A clustering dendrogram was applied to the IRI > 1%items to identify groups of species/size classes using the group average method. A non-metric multidimensional scaling (nMDS) ordination of the masses of the prey items was used for detecting species feeding patterns by size groups. The mass values of the feeding items by fish species and size class were fourth-root transformed and converted into a triangular matrix of similarities among all samples using the Bray-Curtis similarity measure. The most important food items responsible for the sample groupings and for the discrimination between specified groups were identified with the SIM-PER test. The main food items in the groups determined by the cluster analysis were compared using a permutational analysis of variance (PERMANOVA) followed by a posteriori pair-wise test. Moreover, a PERMANOVA was also used to compare the main food items among size classes (Factor: size classes, Levels: 3–4). These latter comparisons were performed based on the Euclidean distance of the mass values of the food items. All these procedures were performed using PRIMER 6.0 + Permanova software (Anderson et al. 2008).

Results

A total of 232 stomachs that had food contents were analyzed, with 99 (size range, 23.6–189.6 mm TL) identified as *Diapterus rhombeus*, 90 as *Eucinostomus argenteus* (21.0–160.0 mm TL) and 43 as *Eucinostomus gula* (55.8–149.8 mm TL). *Diapterus rhombeus* fed on 16 food items, mainly Copepoda Harpacticoida (%IRI = 61.9) and Calanoida (%IRI = 37.1) species. *Eucinostomus argenteus* fed on 12 food items, mainly Bivalvia siphons (%IRI = 56.2), and errant polychaetes (%IRI = 33.3), whereas *E. gula* fed on 15 items, mainly errant polychaetes (%IRI = 62.5%) and Bivalvia siphons (%IRI = 30.6%) (Table 1). Additional information on numbers, masses and frequency of occurrence of the feeding items is given in Table S1 and Figs. S1-S3 [Supporting Information].

Based on the sizes at which most breakpoints were detected, individuals of *D. rhombeus* were classified into four size groups: (1) 42 individuals with <60 mm TL (Dr1); (2) 19 individuals with 60–80 mm TL (Dr2), in which all breakpoints except six occurred; (3) 24 individuals with 80–100 mm TL (Dr3) (breakpoints: 80.8 mm TL for ED, 88.82 mm TL for MH, 89.49 mm TL for MW, 95.23 mm TL for UM,

 Table 1
 Percentage of the index of relative importance (%IRI) of the feeding items for the three species of Gerreidae

Feeding items	D. rhombeus	E. argenteus	E. guld
Nematoda	0.3	0.3	1.7
Sipuncula	<0.1	-	-
Crustacea			
Harpacticoida	61.9	4.5	3.0
Calanoida	37.1	0.8	0.2
Cyclopoida	0.4	1.1	< 0.1
Cumacea	<0.1	_	-
Tanaidacea	_	0.2	0.1
Ostracoda	0.1	2.8	0.5
Mysidacea	<0.1	-	-
Amphipoda	<0.1	<0.1	0.1
Gammaridea	_	-	< 0.1
Isopoda larvae	<0.1	-	-
Caprella	<0.1	-	< 0.1
Crustacea larvae	<0.1	-	-
Crustacea eggs	0.2	-	_
Polychaeta			
Polychaeta (errant)	<0.1	33.3	62.5
Polychaeta (sedentary)	<0.1	0.8	0.8
Polychaeta (tube)	-	<0.1	0.1
Hexapoda			
Insect larvae	-	_	< 0.1
Mollusca			
Bivalvia siphon	<0.1	56.2	30.6
Teleostei			
Teleostei (Scales)	-	<0.1	-
Algae fragment	-	_	0.04

97.36 mm TL for LM, 100.32 mm TL for PW); and (4) 14 individuals >100 mm TL (Dr4) (Table 2).

All breakpoints observed in the morphometric characteristics of *E. argenteus* occurred when individuals had a TL of 62.69-101.36 mm (Table 2). Consequently, three size-groups, corresponding to three size classes in the ontogeny of this species were retained as follows: (1) 38 individuals with <60 mm TL (Ea1); (2) 25 individuals with 60–100 mm TL (Ea2); and (3) 27 individuals with >100 mm TL (Ea3).

For *Eucinostomus gula*, all breakpoints occurred when individuals had a TL of 78.1–85.24 mm TL (Table 2). Therefore, three size-groups, corresponding to three classes in the ontogeny of this species, were retained: (1) 23 individuals with <80 mm TL (Eg1); (2) eight individuals with 80–90 mm TL (Eg2); and (3) 12 individuals with >90 mm TL (Eg3).

Significant differences in diet were found among the size classes for the three fish species according to PERMANOVA (Pseudo- $F_{(9, 225)} = 17.26$; P = 0.001). Most pairwise comparisons detected significant dissimilarities (P < 0.005), except for the size classes within the *Eucinostomus* genus, namely, Ea1 – Eg2 (P = 0.05), Ea2 – Eg1 (P = 0.453), Ea2 – Eg2 (P = 0.084), Ea2 – Eg3 (P = 0.128), Ea3 – Eg3 (P = 0.089), Eg1 – Eg2 (P = 0.96), Eg1 – Eg3 (P = 0.02) and Eg2 – Eg3 (P = 0.22).

Cluster analysis on the %IRI of the three species size classes showed four feeding groups (Fig. 3), which correspond to changes in diet during the growth of the individual. These groups were consistent with the patterns detected by the nMDS analysis (Fig. 4). Group I was formed by the smallest individuals of D. rhombeus (Dr1, < 60 mm TL) alone, which mainly fed on Calanoida copepods (IRI = 80.7%) and, to a lesser extent, on Harpacticoida copepods (IRI = 16.7). Group II was formed by larger individuals of D. rhombeus (Dr2, Dr3 and Dr4, > 60 mm TL) that also mainly fed on copepods, but consumed more Harpaticoida than Calanoida copepods. Groups III (Ea3 and Eg3) and IV (Ea1, Eg1, Ea2 and Eg2) corresponded to larger and smaller individuals of the Eucinostomus genus, respectively. The main food item for group III was Bivalvia siphons (IRI = 94.6% for Ea3; IRI = 86.8% for Eg3), whereas group IV preyed mainly on errant polychaetes. PERMANOVA comparisons detected significant differences among the groups (Pseudo-F = 21.97; P = 0.001), with the most pair-wise differences between the groups II and IV (t = 5.2065; P = 0.033). Moreover, the main

Table 2 Parameters	of piecewise	p-regression	on (regression	1 and regres	ssion 2 su	uccessively)	models	adjusted to the	growth of .	21 measu	ared charact	ers versu	s Total Lengtl	(TL)	
Morphometrics	Diapterus	rhombeu	Sì			Eucinoston	nus argen	snətr			Eucinoston	nus gula			
IIIEASUICIIIEIIIS	Regression	n 1	Breakpoint	Regression	2	Regression	i 1	Breakpoint	Regression	2	Regression	11	Breakpoint	Regression	5
	Intercept	Slope		Intercept	Slope	Intercept	Slope		Intercept	Slope	Intercept	Slope		Intercept	Slope
Head length	0.84	0.21	71.56	0.6	0.24	0.6	0.24	66.5	3.36	0.21	4.07	0.21	84.13	8.53	0.16
Head to pectoral fin	0.76	0.25	70.8	0.76	0.26	0.76	0.26	65.74	2.59	0.24	3.53	0.24	83.97	5.53	0.21
Head to pelvic fin	-0.65	0.31	72.2	0.17	0.32	0.17	0.32	64.1	2.06	0.3	1.18	0.32	85.24	6.58	0.26
Head to anal fin	-0.36	0.49	65.72	-0.03	0.54	-0.03	0.54	63.17	-3.72	0.58	-1.42	0.56	82.17	-1.85	0.57
Head to dorsal fin	1.24	0.29	70.44	0.92	0.30	0.92	0.3	69.26	-1.09	0.31	2.30	0.27	82.92	1.08	0.29
Body depth	-1.69	0.38	67.36	-0.95	0.28	-0.95	0.28	64.44	0.49	0.27	-1.91	0.31	83.06	2.08	0.28
Head height	-0.86	0.25	69.84	-0.40	0.23	-0.40	0.23	65.96	0.80	0.22	-0.37	0.25	83.18	-5.53	0.30
Eye diameter	-0.14	0.09	80.8	0.44	0.09	0.44	0.09	77.88	2.45	0.06	1.03	0.08	84.08	2.50	0.06
Pectoral length	-1.04	0.24	69.22	-1.44	0.23	-1.44	0.23	62.69	-2.82	0.25	-2.67	0.26	82.8	-2.1	0.27
Pectoral height	-0.75	0.07	75.37	-0.45	0.06	-0.45	0.06	81.88	-0.15	0.05	-0.72	0.06	81.94	0.45	0.04
Peduncle depth	0.004	60.0	76.08	-0.28	0.08	-0.28	0.08	74.42	0.25	0.08	-1.11	0.10	83.06	-0.6	0.09
Caudal depth	-4.19	0.26	68.27	-0.84	0.16	-0.84	0.16	63.79	-4.9	0.24	-0.61	0.19	81.19	-8.62	0.29
Caudal length	-1.80	0.32	71.36	-0.93	0.29	-0.94	0.29	65.26	3.16	0.24	1.15	0.26	83.32	2.02	0.25
Body width	0.165	0.08	74.97	0.05	0.09	0.052	0.09	71.69	-3.7	0.13	0.96	0.08	83.13	-3.00	0.13
Peduncle width	-0.09	0.03	100.32	-0.18	0.02	-0.18	0.02	101.36	-1.26	0.03	0.39	0.02	80.77	0.02	0.02
Head width	0.51	0.10	69.32	-0.09	0.12	-0.09	0.12	71.63	-0.26	0.11	1.31	0.09	83.65	0.01	0.11
Mouth width	0.37	0.04	89.49	0.43	0.04	0.43	0.04	87.15	-0.21	0.05	1.33	0.02	83.68	1.23	0.03
Mouth height	0.46	0.04	88.82	0.77	0.05	0.77	0.05	83.54	0.18	0.06	1.43	0.04	83.37	-1.61	0.07
Upper maxilla	0.95	0.03	95.23	0.28	0.07	0.28	0.07	75.51	-0.78	0.09	1.23	0.06	78.1	-1.93	0.09
Lower maxilla	0.64	0.03	97.36	0.26	0.04	0.26	0.04	91.03	0.30	0.04	0.34	0.04	83.41	0.86	0.03
Head to anus	0.49	0.38	68.17	0.35	0.48	0.35	0.48	63.64	-2.61	0.51	3.61	0.43	83.5	-3.34	0.51

Breakpoint: TL values for which the piecewise regression models switched from regression 1 to regression 2



Fig. 3 A dendrogram from cluster analysis on the Index of Relative Importance (%IRI) for feeding items by size class of three species of the Gerreidae Family

food sources also differed significantly between groups II and IV (Table 3), as the case of Harpacticoida (t = 9.46; P = 0.026) and Calanoida (t = 5.85; P = 0.028) copepods, errant polychaetes (t = 23.28; P = 0.021) and Bivalvia siphons (t = 2.43; P = 0.055). The remaining groups did not differ significantly in relation to the main food items.

A decreased niche breadth for the three species was found when they reached larger sizes: *D. rhombeus* (Dr1 = 0.15; Dr2 = 0.06; Dr3 = 0.02 and Dr4 = 0.08); *E. argenteus* (Ea1 = 0.42; Ea2 = 0.41; and Ea3 = 0.02); and *E. gula* (Eg1 = 0.31; Eg2 = 0.14; and Eg3 = 0.03).

Moreover, the number of items preyed on by species of the *Eucinostomus* genus also decreased with growth (Ea1 = 10 items; Ea2 and Ea3 = 9 items; Eg1 = 13 items; Eg2 = 9; Eg3 = 4 items). However, for *D. rhombeus*, the number of items increased with growth (Dr1 and Dr2 = 8; Dr3 = 13; and Dr4 = 12).

A very high degree of intraspecific feeding niche overlap between all size classes of *D. rhombeus* was found, with the Morisita index higher than 0.6 in all pairwise comparisons (Table 4). On the other hand, the size classes of the species of the *Eucinostomus* genus had a low feeding niche overlap according to the

Fig. 4 Ordination diagram of non-metric multidimensional scaling analysis on the f feeding items (in mass) of the species of the Gerreidae family, with samples coded by size classes defined by the breakpoints. Codes – Species: Dr, *Diapterus rhombeus*, Ea, *Eucinostomus argenteus*; Eg, *Eucinostomus gula*. Size range: 1, 2, 3 and 4



Table 3 PERMANOVA results
for comparisons of the main
feeding items among the groups
defined by cluster analysis

Main items	Pseudo-F	Р	Pair-wise significant differences
Harpacticoida	57.80	0.001	II > IV $(t = 9.46; P = 0.026)$
Calanoida	42.29	0.001	II > IV (t = 5.85; $P = 0.028$)
Polychaeta (errant)	131.85	0.001	II < IV $(t = 23.28; P = 0.021)$
Polychaeta (sedentary)	1.5264	0.232	_
Bivalvia siphon	12.261	0.008	II < IV $(t = 2.43; P = 0.055)$

Morisita index, with only two exceptions (Ea2 *versus* Eg1 = 0.87; and Ea3 *versus* Eg3 = 0.67).

Diapterus rhombeus had a specialized feeding strategy according to the Amundsen diagram (Fig. 5), mainly preying on Calanoida copepods followed by Harpaticoida copepods when in the smallest size class (Dr1). As the *D. rhombeus* grew, Harpaticoida copepods became the most important food item, and Calanoida copepods were consumed in a comparatively smaller proportion. In the largest size class (Dr4), this species also consumed errant oplychaetes as a secondary food item. Other items were occasionally found in the stomach contents, reflecting the narrow niche width for this species.

Eucinostomus argenteus and *E. gula* consumed errant polychaetes and Bivalvia siphons as the most important food items. The dominant food item in the smallest class of *E. argenteus* (Ea1) were errant polychaetes, although a few individuals of *E. argenteus* consumed a large quantity of Bivalvia siphons in low frequency. As this species reached a larger size, Bivalvia siphons became the main food item, followed by errant polychaetes (Fig. 5).

Eucinostomus gula tended to specialize as they grew. When in a smaller class size (Eg1), they mainly preyed on errant polychaetes and, to a lesser extent, on Bivalvia siphons, and a few individuals consumed a large quantity of algae. As they grew to a larger class size (Eg2 and Eg3), Bivalvia siphons became the dominant prey, together with errant polychaetes, with few remaining secondary food items (Fig. 5).

The average prey area for items consumed by *D. rhombeus* did not differ among the fish size classes, ranging from 0.05 ± 0.01 in Dr1 to 0.12 ± 0.03 mm² in Dr4 (Fig. 6), whereas the predator mouth area ranged from 4.1 ± 0.1 in Dr1 to 39.2 ± 0.5 mm² in Dr4 (Fig. 6). For the *Eucinostomus* genus, the prey area increased with the predator size classes, with *E. argenteus* showing significant differences among all three size classes (P < 0.01). The smallest size class of *Eucinosotmus gula* (Eg1) mainly preyed on small items (0.48 ± 0.21 mm²) compared with individuals in the largest size classes Eg2 (2.04 ± 1.0) and Eg3 (2.32 ± 0.62) (P < 0.01) (Fig. 6). The mouth area of *E. argenteus* increased from 4.0 ± 0.1 mm² in Ea1 to 34.8 ± 0.2 mm² in Ea3, with a comparatively higher rate than *E. gula* that increased

Classes	Dr_1	Dr ₂	Dr ₃	Dr ₄	Ea_1	Ea ₂	Ea ₃	Eg_1	Eg_2
Dr ₁									
Dr ₂	0.67								
Dr ₃	0.61	1.00							
Dr ₄	0.83	0.96	0.94						
Ea ₁	0.02	0.02	0.02	0.02					
Ea ₂	0.02	0.02	0.02	0.02	0.59				
Ea ₃	0.00	0.00	0.00	0.00	0.01	0.30			
Eg ₁	0.01	0.02	0.02	0.02	0.59	0.87	0.17		
Eg ₂	0.00	0.00	0.00	0.00	0.13	0.38	0.17	0.31	
Eg ₃	0.00	0.00	0.00	0.00	0.02	0.54	0.67	0.34	0.43

Table 4 Overlapping of the feeding niche, according to the Simplified Morisita Index (C_H) for species and size classes of Gerreidae family

Significant overlapping ($C_H > 0.60$) in bold. The codes for fish species and size classes are stated in the Results section



Fig. 5 An Amudsen diagram for trophic strategy for size class of three fish species of the Gerreidae Family. The size classes (Dr1, Dr2 ... Eg2) defined in the results. Dr, *Diapterus rhombeus*; Ea = *Eucinostomus argenteus*; Eg = *Eucinostomus gula*; Feeding items code: Al, Alga; Am, Amphipoda; Bi, Bivalvia siphon; Mo, Mollusca; Ca, Calanoida; Cp, *Caprella*; Cy, Cyclopoida; Cu,

from $10.1 \pm 0.1 \text{ mm}^2$ in Eg1 to $26.3 \pm 0.1 \text{ mm}^2$ in Eg3 (Fig. 6).

Discussion

The resource partitioning for sympatric fish species of the Gerreidae family examined in this study was detected at the genus level, with the species of the *Diapterus* and *Eucinostomus* using different resources, thus confirming the limiting similarity principle. Moreover, different size classes of *Diapterus* had a high overlap in their feeding niches, whereas *E. argenteus* and *E. gula* had a low feeding niche overlap, suggesting a different process in the use of their feeding resources. The cooccurrence of closely related species could lead to interspecific competition and ultimately result in competitive exclusion (Werner and Gilliam 1984; Violle et al. 2011). However, some closely related species can coexist

Cumacea; Ga, Gammaridae; Ha, Harpacticoida; Is, Isopode larvae; Cl, Crustacea larvae; Il, Insecta larvae; My, Mysida; Ne, Nematoda; Os, Ostracoda; Ce, Crustacea eggs; Ep, Errantia Polychaeta; Sp, Sedentary Polychaeta; Si, Sipuncula; Ta, Tanaidacea; Pt, Polychaeta tube

(Kelly and Bowler 2009), as confirmed in the present study. The *Eucinostomus* genus had a low feeding niche overlap at species and size-class levels. On the other hand, a high overlap was found between the size classes of *Diapterus*, with exception of the smallest individuals (<60 mm TL) that had a more generalized diet.

The diets of *D. rhombeus* comprised infaunal and epifaunal invertebrates along with the zooplanckton that are preyed on during the early life stages. This feeding pattern occur in most nearshore coastal fish (Baldo and Drake 2002; Elliott et al. 2002). Overall, marine fish feed on copepods during their juvenile stages and shift to other prey as they grow, with mainly larger and more energetic prey (Shaw and Jenkins 1992; Aarnio et al. 1996; Elliott et al. 2002), thus optimizing energy costs (Schoener 1971). Moreover, these changes in preferential prey with increasing class size was detected for *D. rhombeus*, with shifts from the zooplankton to infaunal and epifaunal prey species, suggest an ontogenetic



Fig. 6 Average and standard error (vertical lines) of prey area (above) and mouth gap area (below) for the three Gerreidae species. Dr, *Diapterus rhombeus*; Ea, *Eucinostomus argenteus*; Eg, *Eucinostomus gula*

migratory behaviour from the pelagic to the benthic habitat.

In the present study, we observed that most of the breakpoints for D. rhombeus were coincident in a narrow size range between 60 and 80 m TL. This can suggest behavioral changes between the groups I and II. We detected the replacement of Calanoida copepods, of which, the great majority are planktonic and are consumed by early juveniles (< 60 mm TL), by Harpacticoida copepods, which are benthic dwelling and are consumed by late juvenile and adults.. Such changes in trophic resources are likely to be associated to some morphological features indicated in the breakpoints, such as an increase in the relative size of head height, body depth, the distance head to anal fin and eye diameter. On the other hand, some features decreased with relative size such as the head width and the peduncle depth. According to Kovač et al. (1999), these features are associated with the visual perception and capacity of food acquisition. According to several studies (e.g., Balon 1986; Norton et al. 1995), these morphological changes occur simultaneously with physiological, anatomical, behavioral changes. Thus, the approach using the breakpoints seems to be more efficient than other conventional methods to categorize size classes.

Eucinostomus argenteus had a diet with a high contribution of Bivalvia siphons (%IRI = 56.2), followed by errant polychaetes (%IRI = 33.3), whereas E. gula fed more on errant polychaetes (%IRI = 62.5%) than Bivalvia siphons (%IRI = 30.6%). There was a low diet overlap between size classes of these congeneric species. Except for Ea2 - Eg1 and Ea3 - Eg3. These shifts in the main prey items of E. argenteus and E. gula suggest some degree of resource partitioning between these morphologically similar species, enabling them to coexist in the bay. Although E. gula prefers Bivalvia siphons and errant polychaetes, some individuals had specialization with high between phenotypic compositions (BPCs), which increased the amplitude of the population trophic niche (Schoener 1971). Such increases in niche breadth may avoid exploitation competition (Wootton 1990). Piet et al. (1999) reported that increases in interspecific competition can lead to an increase in trophic breadth by reducing the use of preferential resources and favouring individuals that use resources previously ignored, easing competition.

The consumption of a portion of polychaetes (e.g., palps) and molluscs (e.g., siphons) by fish species have been reported by several studies (e.g., de Vlas 1979; Lagardère 1987; Beyst et al. 1999). In the intertidal Balgzan area (Wadden Sea), de Vlas (1979) reported that 36% of benthic organisms that have body part consumed by flatfishes undergo regeneration of these parts. The high regeneration capacity of organs, such as polychaetes palps and mollusc siphons, is a continuous source of renewable food without mortality of the prey. Thus, the impact of *E. argenteus* and *E. gula* by feeding on similar feeding items that are continuously renewable decreases the impact on equilibrium maintenance. This also could occur in Sepetiba Bay, which supports these Gerreidae fish to coexist in high abundances.

In general, as fish grow, they are able to ingest larger and consequently more energetic prey, which was observed in this study for *Eucinostomus* species, which had an increase in prey area along the fish growth. Thus, the increase in mouth size seems to favor these species to get larger prey. On the other hand, *D. rhombeus* mainly prey on small prey irrespective of size. This seems to somehow fit in the theory of optimal foraging, proposed by MacArthur and Pianka (1966), which established that the costs involved in the search, capture and manipulation of the prey should not be greater than the energy benefits of the prey. Small prey have comparatively low caloric value and are quickly handled favored by the size of the mouth area, whereas larger prey tend to increase the handle time and the capture success can imply in high energetic cost (Sardiña and Cazorla 2005; Parsons and Robinson 2007). Although further studies are need to explain the different pattern between these two genera, it is likely that *D. rhombeus* take advantage of very abundant copepods in the Sepetiba Bay at a relatively smaller energetic cost, whereas the species of *Eucinostomus* change their diet for more energetic prey (e.g., Polychaeta and Bivalvia siphon) at a higher investment cost.

We also found a clear narrowing in the niche breadth for E. argenteus e E. gula as they grow, with specialization during their ontogeny. Both species used mainly errant Polychaeta and other secondary items in the early juvenile phases then shifting progressively to Bivalvia siphons that together with errant polychaetes are the main feeding items as they reach larger size. Such changes to Bivalvia siphons are likely to be associated to an increase in relative size of the head length and increases in the distances from the head to pectoral and pelvic fins in both species, after a TL of 60 mm in E. argenteus and after 80 mm in E. gula, as indicated in the breakpoints. On the other hand, some features decreased with relative size such as the head height for E. gula (> 80 mm TL), and the caudal depth for E. argenteus (> 60 mm TL) and E. gula (> 80 mm TL). The head height and the caudal depth presented a strong positive allometry after a TL of 80 mm in E. gula. These distinct shifts in diet may coincide with key intervals in ontogeny.

According to Amundsen et al. (1996), populations with wide niche breadth can be composed by individuals with wide or narrow niches, thus defining the contribution of the components within or between phenotypes. In the case of the two species of the Eucinostomus genus, the great majority of individuals are likely to have high between-phenotype components, an indication of opportunism in the group of individuals within the populations that consumed some items in high quantity but at low frequency (e.g. algae and tanaids). The individual feeding specialization detected in some studies have been reported as a way to minimize intraspecific competition (Piet et al. 1999; Bolnick et al. 2003; Matich et al. 2017), thereby increasing the potential success of a given species. Feeding specialization at the individual level in a given population depends on a series of differences in ecological, physiological and/or behavioural factors, such as, the forage rate for encountering a type of prey, the energetic value of the prey and the defenses of the prey against predator (Ward et al. 2006).

For fish populations to persist, habitat must be available in sufficient quality and quantity for the range of activities undertaken during all periods of development. Habitats that enhance the diversity, size ranges and abundance of zooplankton should ensure that sufficient food resources are available to larval and juvenile fish (Nunn et al. 2012). Our results demonstrate trophic partitioning between the two genus of the Gerreidae family, with *D. rhombeus* differing in relation to the two species of *Eucinostomus*. We also can conclude that a specialization strategy focusing on the available resource seems to be more beneficial for the three species of Gerreidae family in Sepetiba Bay than a generalist strategy.

Although we have obtained clear and novel results, some limitations of our study must be considered. We focused on presenting a more detailed description of the diet overlaps among these closely related species during their growth based on an efficient and objective method used to categorize size classes, and we chose the winter as the optimal season because of the stability of environmental variables. Therefore, our findings reflect the winter conditions and might not be applicable to other seasons. Seasonal variation was not the focus of this study. However, seasonal variations in the diet have been reported to have minor importance in this group of fishes (Ramos et al. 2014; Araújo et al. 2016a). Another concern is the low number of examined fish in two size classes of the least abundant species (E. gula). As the breakpoints were used to define the size classes, two of the size classes had less than 20 individuals, which limited our capacity to interpret this part of the data. However, all other size classes for each species had more than 20 individuals, and the overall results were consistent with the raised hypotheses. Thus, we believe that this limitation in the sample sizes of these two size classes did not influence our results.

Araújo et al. (2017) evaluated the ichthyofauna of the inner Sepetiba Bay over three decades and found a decline in richness and abundance of fish species, which may be related to a series of anthropogenic activities that take place in the shoreline of this coastal system, contributing to degradation of the habitat. The environmental conditions of Sepetiba Bay still seem to be suitable for the development of this three species of Gerreidae, suppling food in quantity and quality and diet acts as an important mechanism of allowing intra- and interspecific coexistence. This highlights the need for reformulate conservation policies to guarantee the maintenance of species richness in the area. A more comprehensive knowledge of the trophic relationship among the members of the ichthyofauna in this coastal system is essential to contribute this resources conservation. Understanding food relationship among fish species is crucial to contribute to untangle the functional role of the species in the ecossystems (Cruz-Escalona et al. 2000; Petchey and Gaston 2006). This is a fundamental aspect for the development of management approaches for the conservation of biological diversity.

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