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What matters for intraspecific diet changes: the dietary differences between different areas or the increase in body size? The case of the searobin *Prionotus punctatus* in a tropical bay

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Abstract Resource use diversity occurs when a population is composed of ecologically heterogeneous individuals who use only a subset of the population's resource availability. The aim of this study was to examine the diet of juveniles, sub-adults and adults of *Prionotus punctatus* (40 to 190 mm Total Length - TL) to assess the importance of factors driving intraspecific changes, such as spatial differences in the diet or individual body size changes. The intraspecific trophic strategy was also described. We examined the stomach contents of 210 individuals collected in two zones of a tropical bay (outer and inner) grouped into three size classes (< 90 mm TL, juveniles; 90–140 mm TL, subadults; > 140 mm TL, adults). The Prey-Specific Index of Relative Importance (PSIRI) indicated that Peneidae, Amphipoda (excluding Caprellidae), Mysidacea, Teleostei and Copepoda were the most important food items. The change in the diet during fish growth differed between the two bay zones. In the inner zone, the juveniles fed mainly on Copepoda and Amphipoda (excluding Caprellidae), whereas the adults fed mainly on Teleostei and Peneidae. In the outer zone, the juveniles fed mainly on Mysidacea, whereas the adults fed mainly on Peneidae and Brachyura, with Amphipoda (excluding Caprellidae) being an important prey for individuals in all size classes. Significant differences were detected in the diets among size classes (Pseudo-F = 5.52; $P = 0.003$) but not between the two zones (Pseudo-F = 2.20; $P = 0.113$) according to PERMANOVA. Niche breadth decreased during ontogeny, and the niche overlap among the size classes was low (<0.60), except for subadults and adults (>0.80) in both zones. Together, these observations suggest that the feeding niche in the larger-sized individuals of this species tends to overlap irrespective of the dietary differences between different areas, which can indicate some degree of narrowing in morphological and behavioural features. The increase in body size rather than spatial dietary differences seems to be a major determinant for intraspecific changes in feeding habits. Therefore, diet partitioning along growth, rather than dietary spatial change, seems to be the main mechanism used by this species to decrease intraspecific competition.

Keywords Triglidae · Feeding habits · Bays · Feeding niche · Food resources

Introduction

Fish diet studies generate information that allows for an understanding of inter- and intraspecific interactions and reveals the relationships between fish and the environments in which they live (Elliott et al. 2002; Potter et al. 2015). The fish diet is a result of the interactions of several factors, such as the preference of the species for food, the spatial and temporal availability of the

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resources, and access to food (Ross 1986; Krumme 2009). The analysis of the diet is also fundamental for understanding the processes that regulate the functioning of ecosystems (Medeiros et al. 2017) because the functional role of species in the environment is strongly based on food relationships.

As resource distributions become more heterogeneous, distributions of the organisms that use these resources also becomes heterogeneous, decreasing the likelihood that direct interactions and competition will occur. As competitors gather around a food resource, they deplete the resource and can start competing for individual prey items. When this occurs, competitors are likely to initially select the most profitable food items at the least energetic cost to maximize their net energy consumption rate as predicted by the Optimum Forage Theory (MacArthur and Pianka 1966). Optimal food consumption is related to the energy savings by the predator, reflected in a feeding strategy to search and capture prey and save energetic costs (Pianka 1982). Optimal consumption in a given environment rarely occurs in another environment. The habitat patchiness that characterizes these environments is a challenge to species distribution and resource uses. If competition reduces an individual's feed rate below a critical level, the individual may search for another food resource; as a result, the distribution of individuals in a local population reflects the resource landscape (Fretwell and Lucas Jr 1970; Hossain et al. 2017).

Marine fish benefit from the protection and abundance of food resources in bays and other estuarine areas by optimizing the use of resources, and they are conditioned by environmental constraints or by inter- and intraspecific interactions (Wootton 1991; Pessanha and Araújo 2014). Conspecific individuals are considered ecologically equivalent, although a large number of studies have shown that seemingly generalist species are composed of relatively specialized individuals (Bolnick et al. 2003).

Resource competition promotes niche variation within populations but also shows that increased diversity can arise via behavioural plasticity (Svanbäck and Bolnick 2007). Intraspecific food competition exerts powerful selective forces on individuals, with successful foragers thriving in relation to weaker conspecifics. The resource partitioning theory predicts that whenever a species decreases the use of shared available resources by specializing in a specific resource, conspecific competition will decrease more rapidly than intraspecific competition will increase (Colwell and Fuentes 1975; Ward et al. 2006). It is thought that a similar diversifying effect might occur in response to competition among members of a single species. Individuals may mitigate the effects of intraspecific competition by using alternative resources not used by conspecific competitors.

Ontogenetic dietary changes result in a niche expansion and reduced competition among cohorts. Differences in the physiological abilities among cohorts, particularly in terms of the swimming capacity and mouth and jaw size, allow greater exploration of a variety of habitats and use of larger items (Werner and Gilliam 1984). In addition to their higher physiological abilities, larger fish also have a lower risk of predation (Sogard 1997), allowing them to move more freely throughout the habitat than smaller fish (Mittelbach and Osenberg 1993). However, smaller fish have a more specific metabolism than the larger conspecifics (Werner and Gilliam 1984), which means that they need to feed more frequently and possibly less selectively. Their behaviour, therefore, tends to be less risk averse. Thus, many fish may increase the size of food they consume or change their diet during ontogeny (Ross 1986). The ontogenetic asymmetry can cause an energetic bottleneck between the stages of life caused by intraspecific competition.

Prionotus punctatus is one of the most abundant and frequently found species in Sepetiba Bay, occurring year-round in the system (Araújo et al. 1998; Pereira et al. 2015). This species is a daytime feeder with an afternoon tendency (Soares and Apelbaum 1994) and exhibits large increases in size. Because *P. punctatus* is a sit-and-wait predator that seems to shift in prey choice independent of external drivers (such as habitat use), it is expected to exhibit ontogenetic diet shifts (Jackson et al. 2004). The aim of this study was to investigate the use of Sepetiba Bay food resources by *P. punctatus* in different zones (inner and outer) and to assess whether changes occur in feeding during growth or are determined by spatial dietary differences between different zones. The following questions were postulated: 1) Are there any ontogenetic diet shifts across different size classes? 2) Does the diet overlap differ between the bay zones? We also described the strategy used by this species to explore available resources.

Material and methods

Study area and sample collection

Sepetiba Bay (22°54′-23°04’S; 43°34′-44°10’W) is a semi-enclosed area formed by extensive sand deposition on the coast of the State of Rio de Janeiro (Fig. 1), southeastern Brazil. It has a surface area of approximately 450 km^2 and a mean depth of 8.6 m. This microtidal system has a tidal range of approximately 1 m. Predominant northeasterly and southwesterly winds activate thermal currents between the bay and the ocean. The mean water temperature ranges from 21.5 °C in the winter to 26.5 °C in the summer. The bay has two different zones (Fig. 1) that are geographically continuous but differ in depth, salinity gradient and the level of human influences (Araújo et al. 2002; Azevedo et al. 2006). The inner zone is influenced by discharges of perennial small rivers that contribute to increased turbidity and temperature and decreased salinity; the substratum is mainly muddy with depths that are mostly <5 m, and it has an average salinity of 28 ± 1.1. This zone is the most altered because of the nearby industrial development (Cunha et al. 2006; Leal Neto et al. 2006). The outer zone, located near the sea, has comparatively less influence on anthropogenic activities and exhibits contrasting environmental conditions: the substratum is predominantly sandy, the water temperature is comparatively lower, and the salinity and transparency are comparatively higher; the maximum depth is ca. 30 m, and the average salinity is 33 ± 0.9.

Fish were collected quarterly (seasonally) from October 1998 to September 1999 by bottom trawling. The net was 12 m long and had a 25-mm mesh at the wings and a 12-mm mesh at the cod end. The length of the ground rope was 8 m, and the head rope was 7 m. The samples were taken at speeds between 2 and 2.5 knots during a 20 min period, covering an extension of ca. 1.5 km, with the swept area corresponding to approximately 6000 m^2.

The collected fish were fixed in 10% formaldehyde and transferred to 70% ethanol after 48 h. All fish were measured (Total Length, TL in millimetres) and

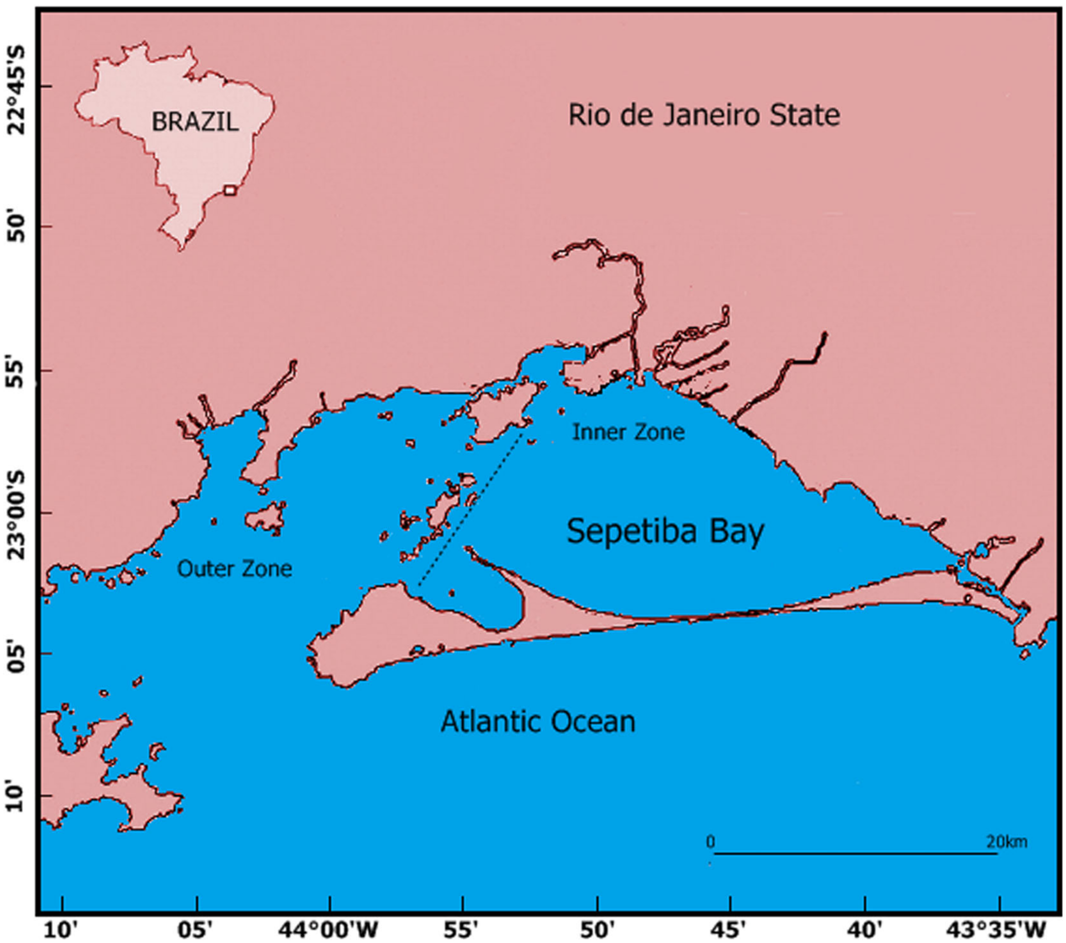

Fig. 1 Map of the study area showing the different zones (Inner and Outer) of the Sepetiba Bay, Brazil

weighed (in grams). The specimens were dissected and their stomachs were removed. The stomach contents were kept in 70% ethanol and examined under a stereoscopic microscope (40x). Prey items were identified at different taxa levels, e.g., Teleostei at the species level, Crustaceans Decapoda at the family level, microcrustaceans at the order level and polychaetas and mollusks at the class level. Empty stomachs or those with unidentifiable contents were later excluded from the analyses. Each food item was identified, 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.

Data handling

The stomach contents of 210 individuals measuring between 40 and 190 mm of total length were analysed. Only eighteen stomachs were empty and were not included in the analyses. Size-related changes in the diet were evaluated considering three classes based on species L_{50} (size at first maturation, $L_{50} = 120–130$ mm for both sexes, see Magro et al. 2000). The classes were I (juveniles <90 mm, size smaller than the first maturation), II (subadults 90–140 mm, size encompassing the first maturation) and III (adults >140 mm, size larger than the first maturation). Individuals in all size classes occurred in both bay zones (inner and outer).

The Prey-Specific Index of Relative Importance (expressed as %PSIRI) proposed by Brown et al. (2012) was used to determine the most important feeding items because it proved to be more robust and produced more congruent results compared with the %IRI. It was calculated for each prey as follows: %PSIRI = (%FO × (%N + %W)) / 2 where %N is the percent of the total number of a given food item, %W is the percent of the total weight, and %FO is the frequency of occurrence.

Levin's standardized index and Morisita's overlap index (Krebs 1999) were calculated for dietary niche for each size class and bay zone. The niche overlap was considered significant when it exceeded the value of 0.6, as suggested by Labropoulou and Eleftheriou (1997). The trophic strategy was assessed with the Costello graphical method (Costello 1990) modified by Amundsen et al. (1996), which considers the average specific weight (ASW) of fish that consumed a specific food item and the food item's percentage frequency of occurrence (%FO). The %ASW was plotted against the %FO and interpreted with respect to its position on the graph.

Statistical treatment

The permutational multivariate analyses of variance (PERMANOVA) was used to compare the composition of the diet among the size classes (three fixed levels: classes I, II and III) and zones (two fixed levels: inner and outer) with seasons (nested in zone) as a random factor. PERMANOVA was performed on a Bray-Curtis similarity matrix with data previously transformed by the fourth root. The volume of each food item was the dependent variable. Statistical significance ($P < 0.05$) was tested using 9999 permutations of residuals under a reduced model of sum of type I (sequential) squares (Anderson et al. 2008) When significant differences were detected ($P < 0.05$), pairwise comparisons between groups were conducted. Non-metric multidimensional scaling (nMDS) was used to evaluate eventual patterns based on the volume of food consumed in regard to size and bay zones. These analyses were performed using the statistical package PRIMER 6.0 with PERMANOVA+1 (Anderson et al. 2008; Clarke and Gorley 2015).

Results

Thirteen food items were identified, but only five were highly important with a %PSIRI >30% in a given zone or size class: Peneidae (shrimps), Amphipoda (excluding Caprellidae), Mysidacea, Teleostei and Copepoda (Table 1). The food item Teleostei encompassed both the identified fish species *Genidens genidens* (Cuvier, 1829), *Menticirrhrus americanus* (Linnaeus, 1758), *Achirus lineatus* (Linnaeus, 1758) and *Citharichthys spilopterus* (Günter, 1862), specimens of the family Gobiidae, and fish that were not identified due to a high degree of digestion that did not allow identification at the species level.

Significant differences in the diet composition were found between size classes ($P = 0.003$) and season (nested in zone) ($P = 0.001$), but not between the bay zones ($P = 0.113$) (Table 2). In addition, interactions between size classes and season (nested in zone) were also significant ($P = 0.001$) according to PERMANOVA (Table 2). Significant results of pairwise comparisons were found between size classes, except between sub-

Table 1 Prey-Specific Index of Relative Importance (%PSIRI) for food items of *Prionotus punctatus* by size classes in the different bay zones of the Sepetiba Bay, Brazil

Items	Inner zone			Outer zone		
	Class I	Class II	Class III	Class I	Class II	Class III
Amphipoda Not Caprellidae	24.1	**30.9**		**33.9**	28.8	**37.6**
Mysidacea	9.3	6.1	3.3	**40.7**	**34.8**	0.3
Peneidae	10.8	24.2	26.7	1.0	**30.1**	**39.6**
Teleostei	1.9	8.9	**49.8**	0.9	1.1	
Achirus lineatus			1.8			
Citharichthys spilopterus				0.3		
Genidens genidens			5.5			
Menticirrhus americanus			2.8			
Gobiidae	1.5		19.1			
Not Identified	0.4	8.9	20.6	0.6	1.1	
Copepoda	**37.9**	3.9	1.1	0.1		
Brachyura	2.9	19.0	15.8	0.9	2.4	20.7
Caprellidae	10.0	6.2	3.3	0.8	1.2	1.1
Cumacea	0.4	0.5		8.8	0.9	0.3
Ostracoda	0.5			0.4		0.3
Isopoda	0.8			9.9	0.1	
Larvae of Brachyura	0.7	0.3		2.6	0.2	
Polychaeta	0.7				0.2	
Bivalvia					0.2	

Most important items (>30%PSIRI) in bold

adults and adults ($P = 0.082$). Seasonally, dietary differences were not found between spring and autumn ($P = 0.709$) for the inner zone and between summer and autumn ($P = 0.095$) for the outer zone. The largest estimated component of the variance (ECV), which represents how important each term is at explaining the overall variation in the model was 21.5% for size, 13.6% for zone, 21.6% for season (nested in zone), and the residuals were 49.8% (Table 2).

In the inner zone, the juveniles fed mainly on Copepoda and Amphipoda not Caprellidae (Fig. 2). Those items were replaced by Teleostei (%PSIRI = 49.8) and Peneidae (%PSIRI = 26.7) in adult individuals (Fig. 2, Table 1). In the outer zone, Amphipoda (excluding Caprellidae) were largely consumed by all size classes (juveniles to adults, %PSIRI = 28.8–37.6), whereas Mysidacea were consumed largely by the juveniles (Class I, %PSIRI = 40.7) and subadults (Class II, %PSIRI = 34.8) (Fig. 2). Adult individuals consumed large amounts of Peneidae (%PSIRI = 39.6) and Brachyura (%PSIRI = 20.7). Items of small size, such as Cumacea and Isopoda, were consumed in comparatively small amounts by juveniles (< 90 mm TL).

Size-related changes in diet were found according to nMDS ordination, with each sample of juvenile individuals clustering separately from the samples of subadult and adult individuals (Fig. 3). On the other hand, samples of the individuals from the inner and outer zones were spread across all diagrams, suggesting that several food items are common in individuals of both bay zones.

The niche breadth in the inner zone was 0.30 in individuals of Class I and decreased to 0.19 in Class II and to 0.12 in Class III. In the outer zone, the niche breadth also decreased from 0.17 in individuals of Class I to 0.11 in Class II and to 0.07 in Class III. Diet overlap between the size classes was low (<0.6) in both zones, with the exception of classes II and III (>0.8).

Most of the food items in the individuals of the inner zone were located in the left part of the Amundsen diagram, indicating that these individuals have a generalist-opportunist feeding strategy (Fig. 4).

Table 2 PERMANOVA summary for comparisons of the diet of *Prionotus punctatus* between size classes and zones (fixed factors) and season (nested in zone) as a random factor in Sepetiba Bay, Brazil

Source	df	MS	Pseudo-F	P(perm)	ECV
Size	2	24,109	5.52	0.003	21.5
Zone	1	21,754	2.20	0.113	13.6
Season (zone)	6	11,401	4.60	0.001	21.6
Size × Zone	2	6162	1.41	0.162	9.2
Size × Season (Zone)	11	4832	1.95	0.001	18.2
Residuals	169	2478			49.8
Total	191				

df, degree of freedom; *MS*, mean square; *ECV*, estimated component of variance

Individuals in Class I tended to feed in a low %FO and a high average specific weight on Peneidae, Isopoda and Amphipoda and comparatively more frequently on the larvae of Brachyura, Mysidacea and Caprellidae. Individuals in Class III fed in a high average specific weight and frequency between 25 and 50% on Teleostei, Peneidae and Brachyura. In the outer zone, a trend for specialism (high frequency and average specific weight)

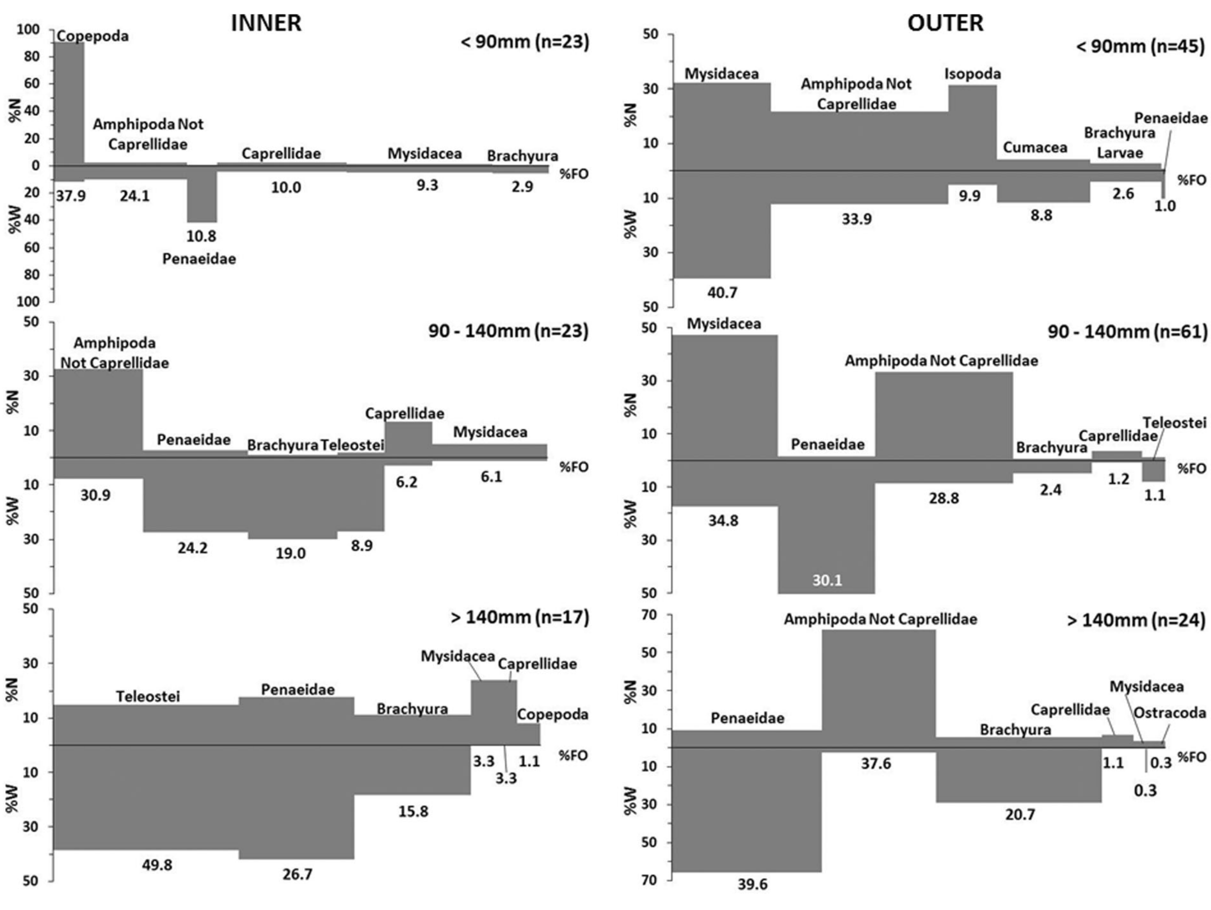

Fig. 2 Prey-Specific Index of Relative Importance (%PSIRI) for the main food items in diet of different size classes of *Prionotus punctatus*, in the Inner (left) and Outer (right) zones of the Sepetiba Bay, Brazil. % N, percentage of number; %W, percent of weight; and %FO, frequency of occurrence. %PSIRI is indicated at the bottom of the rectangles

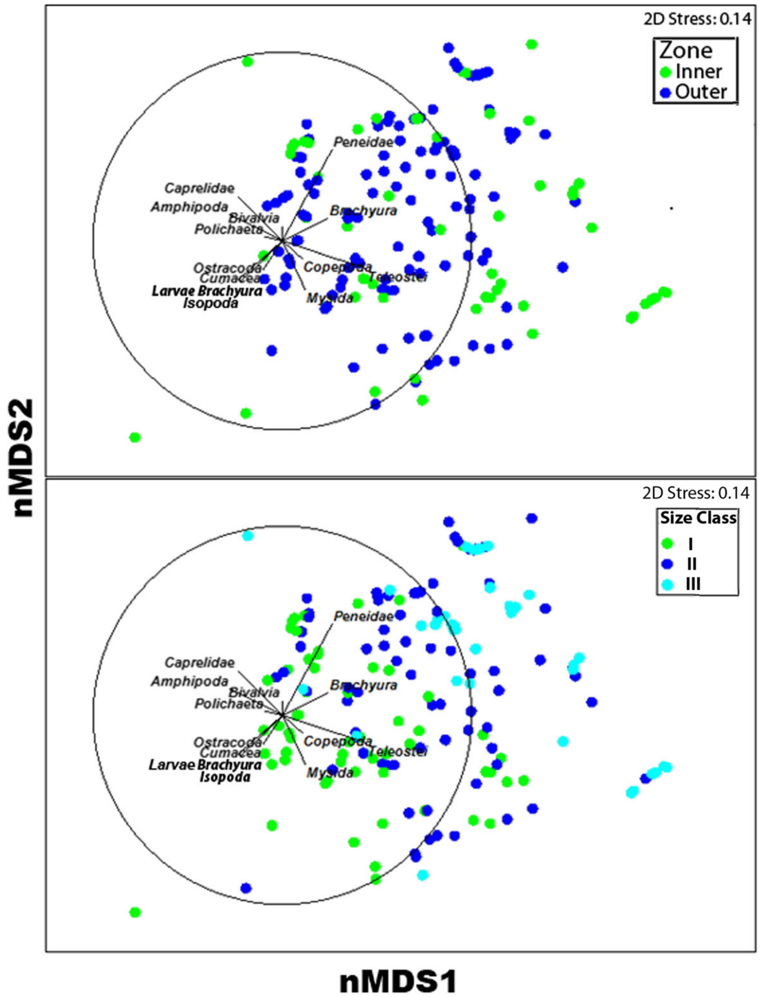

Fig. 3 Diagram of the first two axes of ordination from non-metric Multidimensional Scaling (nMDS) on the diet of *Prionotus punctatus* in the Sepetiba Bay, Brazil, with samples coded by bay zones (inner, outer) and size classes; Class I, juveniles; II, sub-adults; III, adults

was detected with individuals in Class I feeding on Amphipoda, changing to the largest individuals (Class III) feeding on Peneidae and Brachyura.

Discussion

Increases in body size, rather than dietary differences between zones, seem to be the main factor determining intraspecific diet changes in *P. punctatus* in Sepetiba Bay. A marked change in diet was found with the smallest individuals who fed on small-sized crustaceans (Amphipoda and Mysidacea), whereas the adult individuals preyed on large crustaceans (Peneidae and Brachyura) and Teleosts. Dietary changes during ontogenetic development are expected for most Teleostei and are associated with changes in the morphological structures of capture and food intake. The preference for crustaceans was recorded for this species, which seems to be conditioned on the limited capacity of pursuing very mobile prey, such as Teleostei. Although Teleostei have a higher energy content than crustacean, the latter are more difficult to handle and ingest than fish and require longer handling times, which results in lower profitability (Scharf et al. 2000).

The preference for predation on Decapoda crustaceans seems to confirm the tendency to consume slow-moving benthic organisms (Schmitter-Soto and Castro-Aguirre 1996). The Triglidae family is characterized by slow-moving fish with efficient sense organs, such as taste buds, at the free-spine ends of the pectoral fins (Bardach and Case 1965). Species of this family are opportunistic predators that use the modifications of pectoral fins provided with chemoreceptor and tactile

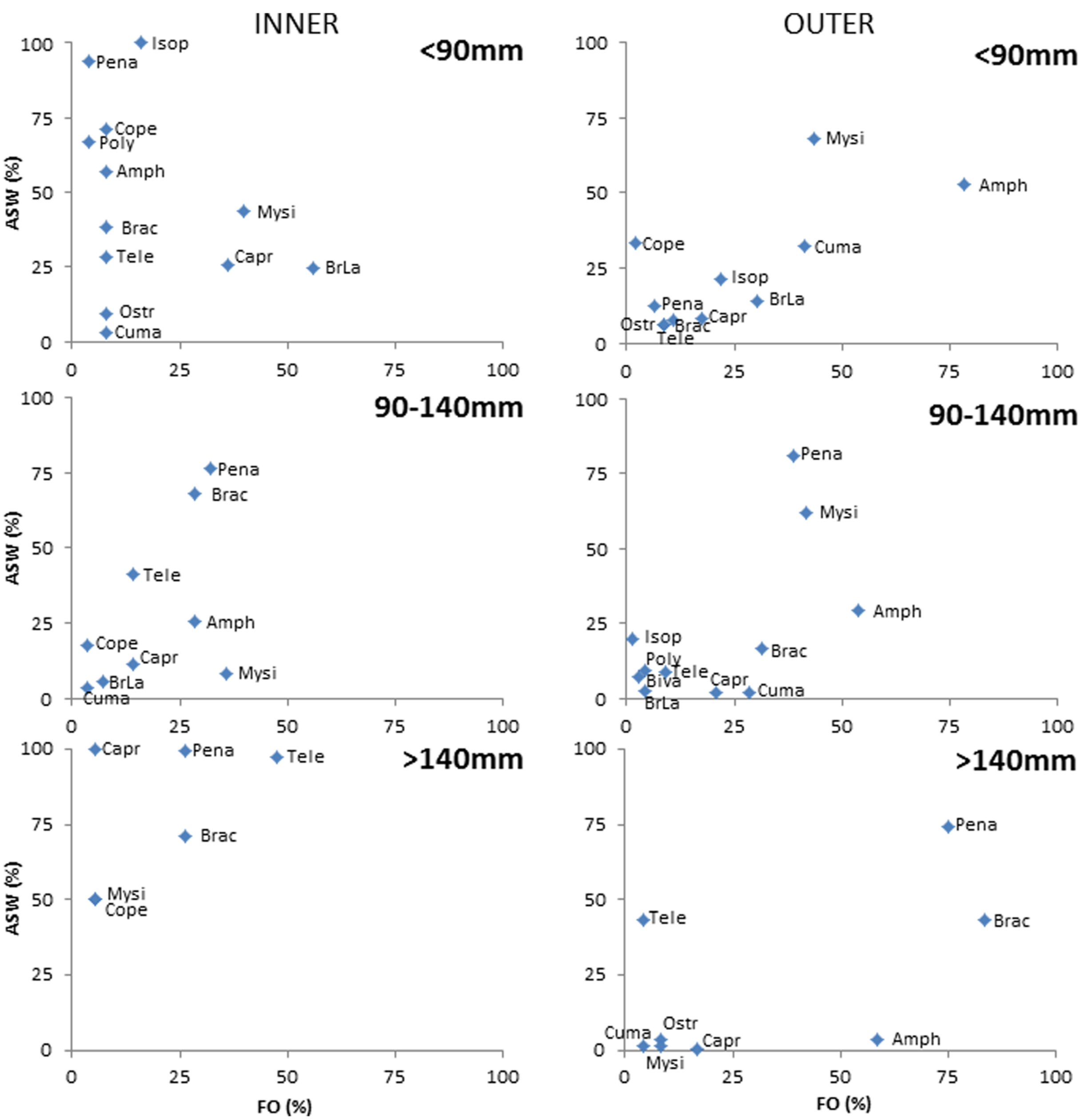

Fig. 4 Diagrams of the trophic strategy (Amundsen) as a function of the Frequency of Occurrence (%FO) and Average Specific Weight (%ASW), for the different size classes and zones of the Sepetiba Bay, Brazil. Legend: Amph, Amphipoda Not Caprellidae; Capr, Amphipoda Caprellidae; Biva, Bivalvia; Brac, Brachyura; BrLa, Brachyura Larvae; Cope, Copepoda; Cuma, Cumacea; Isop, Isopoda; Mysi, Mysidacea; Ostr, Ostracoda; Pena, Peneidae; Poly, Polychaeta; Tele, Teleostei

mechanisms in the search of their prey (McBride and Able 1994). In general, Amphipoda, not Caprellidae and Mysidacea, are abundant and widely available as a resource used throughout Sepetiba Bay and may be suitable as the most important source of energy for small fish, whereas the decapods Brachyrura and Peneidae are the most important feeding items for larger fish (Guedes et al. 2015). Larger juveniles have larger jaw widths, more developed mandibular structures, better visual acuity, and swim faster than smaller conspecifics. Collectively, these attributes allow fish of a certain size to expand their trophic niche (Scharf et al. 2000).

The preference of *P. punctatus* to feed on crustaceans has already been observed in other areas, such as the southern coast (latitude 32–33°S) of Brazil (Teixeira and Haimovici 1989), where the crab *Portunus spinicarpus* and the shrimp *Pleoticus muelleri* were the most important prey. Peneidae and Caridea prawns and Amphipoda were also reported as the main food items for *P. prionotus* on the northern coast of São Paulo State (latitude 23–25°S) (Braga and Braga 1987; Soares and Apelbaum 1994; Muto et al. 2014). On the north coast of the state of Rio de Janeiro (latitude 22°S), *P. punctatus* has been reported as having a carcinophagous feeding habit with a preference for Isopoda and Cumacea (São Clemente et al. 2014).

Significant interactions in the diets of individuals between size classes and season (nested in zone) detected in this study suggest the opportunistic feeding strategy of this species, especially in the individuals of the smallest size. Changes in dietary habits between the size classes and season (nested in zone) may be a mechanism to reduce intraspecific competition, thus facilitating intra- and interspecific coexistence. Although seasonal variation was not the focus of this study, we found indications of seasonal changes that should be addressed in further studies.

It seems that *P. punctatus* has a trend for generalism-opportunism in the inner zone and for specialism in the outer zone. Whereas most items are consumed in a high average specific weight and low frequency (opportunism) in the inner zone, specialism (high weight and high frequency) of Amphipoda (not Caprellidae) in small individuals and of Peneidae and Brachyura in the largest individuals was detected in the outer zone. The causes of changes in feeding strategy are difficult to detect, and biotic interactions with other fish species may be part of the explanation. In addition, the comparatively lower salinity in the inner zone could influence the low availability of those crustaceans compared with the salinity of the outer zone that is near marine conditions. *Prionotus punctatus* is more abundant in the outer zone of Sepetiba Bay, where environmental conditions of high salinity and depth have more influence on marine waters (Milagre et al. 2002). The specialist strategy in this area seems to be a mechanism for the use and partitioning of resources with other marine species. Only the largest individuals seem to explore the opportunist strategy when they penetrate the inner zone and prey on Teleosts, a more energetic and profitable prey.

The availability of prey can be considered one of the most important components of habitat quality and could be one of the most important factors influencing the distribution of fish at the local scale (Hinz et al. 2003). Additionally, most species change their diet with size and age (Day et al. 1989; Platell et al. 1997; Litz et al. 2017). Ontogenetic changes in diet are important to reduce the intra- and interspecific competition of fish (Elliott et al. 2002). In this study, dietary changes and a reduction of the trophic niche breadth, together with a high niche overlap, were observed during growth. The larger dietary breadth of juveniles may be due to the requirements of more energy for growth, and preference for small food items can reflect the inability of these individuals to capture the food items present in the diet of adults and indicate the higher protein needs of juveniles. Niche overlap manifests more frequently when food is more abundant and becomes less evident when food is limited (Pianka 1982). Additionally, within a geographical area, individuals of a given species but of different size classes can occupy diverse trophic niches to seek appropriate prey and/or facilitate coexistence with their conspecifics. Together, these observations suggest that this species tends to overlap the feeding niche of larger-sized individuals irrespective of food availability, which can indicate some degree of narrowing in morphological and behavioural features.

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