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## André Luiz Machado Pessanha & Francisco Gerson Araújo

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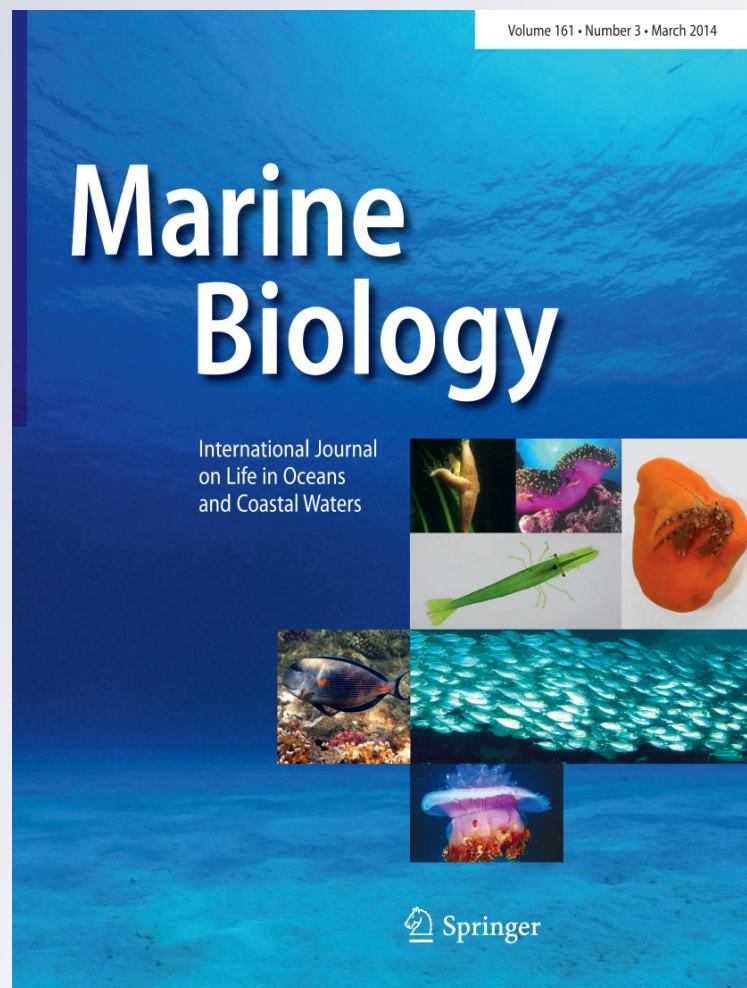
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# Shifts of the feeding niche along the size dimension of three juvenile fish species in a tidal mudflat in southeastern Brazil

**André Luiz Machado Pessanha · Francisco Gerson Araújo**

**Abstract** The diet of three cooccurring abundant fish species (*Eucinostomus argenteus*, *Diapterus rhombeus* and *Micropogonias furnieri*) and its ontogenetic changes in a mudflat area of a tropical bay in southeastern Brazil were described. The working hypothesis is that these three species shift the use of the available resources throughout their growth. Early juveniles of *D. rhombeus* and *M. furnieri* fed mainly on Cyclopoida copepods, shifting to Nematoda (*D. rhombeus*) and errant Polychaeta (*M. furnieri*) as they increased in size. In contrast, the early life stages of *E. argenteus* fed mainly on errant Polychaeta and Calanoida copepods, with increasing niche breadth as they grew. The relative degree of individual specialisation in resource use indicated specialism for *M. furnieri* and *E. argenteus*, and generalism for *D. rhombeus*. The largest intraspecific overlap was found for the smallest size classes. Niche breadth increased during ontogeny, with a higher average niche breadth at lower prey length/predator length ratios. Therefore, species-specific differences in diet across the resource gradient and increased niche breadth during ontogeny characterised the shifts of resource use, and probably account for the coexistence of these species in zones of sympatry in mudflat areas of southeastern Brazil.

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## Introduction

A description of the trophic relationships among juvenile fish species is fundamental for understanding their functional role in the ecosystem (Meng and Powell 2003; Hajisamae 2009; Florin and Lavados 2010). Competition can increase the diversity of resource use within a natural population because coexisting species evolve to use different resources, thereby reducing the effects of interspecific competition (Ross 1978; Schmitt and Coyer 1982; Mittelbach et al. 1988; Uiblein 1991). Although ecologists have traditionally assumed that conspecific individuals are ecologically equivalent, a large number of studies have shown that each population appears to be composed of both relatively generalised and relatively specialised individuals (Bolnick et al. 2003). This pattern occurs if a population is 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 intraspecific competition if they use alternative resources not used by conspecific competitors (Schoener 1971; Svanbäck and Bolnick 2007).

Ontogenetic niche shifts, defined as changes in resource or habitat use during the course of an individual's lifetime, are prominent features in the ecology of many size-structured populations (Werner and Gilliam 1984). Because the diets of coexisting fish species also frequently undergo ontogenetic changes (Werner and Gilliam 1984; Ross 1978; Scharf et al. 2000), the extent to which dietary overlap occurs within and between species will most likely vary with body size. Size-related diet shifts are the result of size-specific changes in foraging ability. These changes enable individuals to capture and consume progressively larger prey (Holbrook and Schmitt 1992; Schafer et al. 2002). If ontogenetic niche shifts are relatively discrete, a population

can be divided into separate size classes (or stages) based on diet or habitat use (Muñoz and Ojeda 1998; Osenberg et al. 1992). Although the consequences of ontogenetic niche shifts for intra- and interspecific interactions in size-structured populations of fishes have been investigated experimentally (e.g., Olson et al. 1995; Olson 1996), these studies have concentrated on only one or two species, and the implications of niche shifts during the ontogeny of fish species have seldom been investigated. Our understanding of how these factors influence transitions between stages is primarily derived from theoretical work (Taper and Case 1985; Mittelbach et al. 1988). Clearly, there is a need for additional empirical studies on stage-structured populations.

Sepetiba Bay (22°54′–23°04′ S; 43°34′–44°10′ W) is a sedimentary embayment on the coast of Rio de Janeiro State in Southeastern Brazil. The bay has a surface area of approximately 450 km$^2$ and is open to the Atlantic Ocean on its western boundary. This microtidal system is predominantly polyhaline (salinity average = 30 ‰) and the mean temperature ranges from 21.5 °C in winter to 26.5 °C in summer (Araújo et al. 2002). Its inner zone includes an extensive area of mudflat formed by sediment deposition from rivers and other small continental drainages (Signorini 1980). This particular type of habitat is of key importance for the estuarine food web due to its high productivity (Degre et al. 2006). The species use the area because they can benefit from the substantial advantages furnished by the habitat, i.e., high productivity, abundance of food resources, and refuge provided by shallow intertidal waters (Paterson and Whitfield 2000; Kanou et al. 2004; Vinagre et al. 2006). Indications of the importance of Sepetiba Bay mudflats for recruitment and as rearing grounds for several species of fishes have been furnished by several studies (e.g., Araújo et al. 2002; Pessanha and Araújo 2003; Guedes and Araujo 2008). Three fish species are dominant in the Sepetiba Bay mudflats, ranking as the top abundant species in both numbers and biomass: *Micropogonias furnieri* (Desmarest, 1823) (Sciaenidae), *Diapterus rhombeus* (Cuvier, 1829) (Gerreidae), and *Eucinostomus argenteus* (Baird and Girard, 1855) (Gerreidae). Collectively, these species represent 82.0 % of the total number of fishes collected and 82.1 % of the total biomass (Pessanha et al. 2003). These three species play an important role in the trophic dynamics of the inner Sepetiba Bay (Araújo and Santos 1999; Costa and Araújo 2003; Vicentini and Araújo 2003) because they use the area during their early life cycle, with the adults reproducing in deeper areas nearby. Understanding how these three abundant species use the available resources in this tidal mudflat area and identifying the strategy that is developed to allow the species to coexist during their early life are important because the functional roles of fishes are based on feeding

relationships (Hajisamae et al. 2003; Degre et al. 2006). This study aimed to describe the diets of the three species and to investigate the eventual shifts of the feeding niche along the size dimension during their early life. The working hypothesis is that these three species shift the use of the available resources throughout their growth.

## Materials and methods

### Sampling and data handling

The fishes were sampled using a beach seine net (10.0 m × 2.5 m; 7 mm mesh size). Hauls were 30 m long, and the net was used at a depth of approximately 1.5 m. The area seined (300 m$^2$) and the time (10 min) allocated for each haul were standardised to allow comparisons among collections. All samples were collected during spring tide near the day of the full moon. Immediately after collection, all individuals of the three target species were anaesthetised 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 species, measured for total length—TL—(in millimetres), and weighed (in grams) after preservation. Stomachs were removed and food items were analysed from a sub-sample of the fish captured. If a sample consisted of less than 30 fish, all stomachs were dissected and examined. In samples with more than 30 fish, 30 individuals covering a wide range of sizes were selected for dissection in each month. Empty stomachs or those with unidentifiable contents were later excluded from the analyses. Each food item was identified to the lowest taxonomic level possible under a stereomicroscope, counted, and weighed to the nearest 0.001 g. A subset of up to 20 randomly selected individuals was selected to measure prey body length to the nearest 0.01 mm (Ojeda and Dearborn 1991).

### Data analyses

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 for the diet in terms of the frequency of occurrence (%FO) and of the percentage composition by number (%N) and by mass (%M) (Hyslop 1980): IRI = (%N + %M) × %FO. The index for each prey item was expressed as a percentage of the sum of all IRI scores: %IRI = (IRI/Σ IRI) × 100. The IRI was not calculated for items that were not individually counted or weighed, such as fragments of Cirripedia, diatoms, and algae. Only items with an IRI >1 % were shown.

**Table 1** Number of analyzed fishes, mean total length (mm), and mean total weight (mm)

| Species | Micropogonias furnieri | Diapterus rhombeus | Eucinostomus argenteus |
|---|---|---|---|
| Number of individuals | 414 | 135 | 255 |
| Number of stomachs with contents | 327 | 62 | 138 |
| Mean total length (±SD) | 34 (±12) mm | 32 (±5) mm | 33 (±6) mm |
| Mean total weight (±SD) | 4 (±1) g | 3 (±2) g | 3 (±2) g |

To assess possible changes in diet with respect to size, fish were divided into three size classes that were assigned according to predefined size ranges: Total Length$_1$ (TL$_1$) ≤30 mm; TL$_2$ = 31–40 mm; TL$_3$ >40 mm. All individuals were juveniles and had a very similar average size with the largest ones measuring less than 70 mm TL.

A matrix of food items was constructed to reduce the number of samples to facilitate the detection of feeding patterns, as described by Schafer et al. (2002). For each species and size class, the stomach contents of 3–5 individuals were grouped, and the number and weight of the items in the group were averaged to represent a single sample. According to Platell and Potter (2001), pooling the stomach content of 3–5 individuals avoids the potential bias introduced by individuals that have low numbers of small food items. This procedure was used to assess diet by species and size class only. For assessing the trophic strategy and individual specialisation, each individual was taken as a sample unit.

The numerical abundances for the feeding data values for each sample by species and size class were square-root transformed and converted into a triangular matrix of similarities among all samples, using the Bray–Curtis similarity measure (Schafer et al. 2002). The diet composition was compared among the three species with an ANOSIM procedure. A significance level of $P < 0.05$ was used (Hourston et al. 2004). The food items responsible for the sample groupings and for the discrimination between specified groups were identified with the SIMPER routine. The Bray–Curtis similarity matrix was also used to construct the clustering dendrogram, which used the group average as a method to identify clusters of species and size classes. The ANOSIM and SIMPER procedures were performed with the PRIMER software package, version 5.0 (Clarke 1993).

Trophic strategy

The relative degree of individual specialisation was measured as the proportion of total niche breadth (TNB) explained by within-individual component (WIC) variation (Roughgarden 1972). As this value approaches 1, all individuals utilise the full range of the population's niche, whereas smaller values indicate decreasing interindividual

overlap and hence higher individual specialisation (Bolnick et al. 2002).

The numerical data obtained for the food items were used to calculate the Shannon-Wiener diversity index as a proxy of the niche breadth. A Kruskal–Wallis test was used to compare niche breadth among the size classes for each species. The simplified Morisita overlap index (Krebs 1989) was used to assess niche overlap among species and size classes. Values of the overlap index greater than 0.60 were considered biologically significant (Labropoulou and Eleftheriou 1997). The simplified Morisita index was also calculated based on the numerical data for the food items. The prey size data were converted to a ratio scale by dividing each prey size by the respective predator size. The average prey/predator size ratio was then plotted against the average trophic-niche breadth to evaluate whether a general size-based trend was apparent (Scharf et al. 2000).

**Results**

Diet

The three fish species were all represented by juveniles and had a very similar average size (Table 1) ranging from 32 (17–50) mm for *D. rhombeus* to 34 (15–68) mm total length for *M. furnieri*. *E. argenteus* had an intermediate average size of 33 (16–51) mm total length. The diet was composed mainly of benthic (errant Polychaeta, Ostracoda and Nematoda) and planktonic organisms (Calanoida and Cyclopoida, fish eggs) (Table 2). *M. furnieri* fed primarily on errant Polychaeta and Cyclopoida; *D. rhombeus* fed primarily on Cyclopoida, Calanoida, Ostracoda, and errant Polychaeta; and *E. argenteus* fed primarily on Calanoida and errant Polychaeta (Table 2).

Significant differences in diet were found among the three fish species according to ANOSIM ($R$ Global = 0.437; $P = 0.001$). The highest level of similarity was recorded between *M. furnieri* and *D. rhombeus* ($R = 0.136$; $P = 0.001$), and the greatest differences were found between *D. rhombeus* and *E. argenteus* ($R = 0.658$; $P = 0.001$) and between *M. furnieri* and *E. argenteus* ($R = 0.550$; $P = 0.001$). The food items that most

**Table 2** Frequency of occurrence (%FO), numeric percentage (%N), mass percentage (%M), and the percentage of the index of relative importance (%IRI) of the feeding items for *M. furnieri*, *D. rhombeus,* and *E. argenteus* in a tidal mudflat in Sepetiba Bay, Brazil

| Feeding items | *Micropogonias furnieri* | | | | *Diapterus rhombeus* | | | | *Eucinostomus argenteus* | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | %FO | %N | %M | %IRI | %FO | %N | %M | %IRI | %FO | %N | %M | %IRI |
| Nematoda | 0.9 | 0.1 | 0.8 | <0.1 | 4.7 | 0.3 | 2.0 | 1.4 | 5.1 | 12.7 | 5.3 | 1.4 |
| Crustacea | | | | | | | | | | | | |
| Harpacticoida | 0.9 | 0.5 | 0.8 | <0.1 | 7.9 | 0.1 | 3.4 | 0.1 | 8.7 | 1.0 | 8.2 | 1.3 |
| Calanoida | | | | | 28.5 | 29.4 | 20.6 | 15.3 | 50.3 | 39.1 | 25.7 | 52.6 |
| Cyclopoida | 29.3 | 53.1 | 18.7 | 28.1 | 61.9 | 56.8 | 27.9 | 56.1 | 5.1 | 1.9 | 5.3 | 0.5 |
| Tainadacea | 0.9 | <0.1 | 0.8 | <0.1 | – | – | – | – | – | – | – | – |
| Cladocera | 4.0 | 1.3 | 3.6 | 0.1 | 3.1 | <0.1 | 1.3 | <0.1 | – | – | – | – |
| Ostracoda | 0.9 | <0.1 | 0.2 | <0.1 | 47.6 | 5.8 | 20.6 | 13.4 | 10.9 | 2.9 | 9.8 | 2.2 |
| Mysidacea | 2.1 | 0.26 | 2.0 | <0.1 | – | – | – | – | – | – | – | – |
| Crustacea larvae | 0.3 | <0.1 | 0.3 | <0.1 | – | – | – | – | 2.9 | 0.2 | 2.2 | 0.1 |
| Polychaeta | | | | | | | | | | | | |
| Errant | 54.7 | 40.9 | 55.7 | 70.5 | 46.0 | 6.6 | 20.3 | 13.2 | 63.5 | 8.2 | 29.7 | 38.8 |
| Sedentary | 8.7 | 2.7 | 3.9 | 0.3 | | | | | | | | |
| Sipuncula | 0.3 | <0.1 | 0.3 | <0.1 | – | – | – | – | – | – | – | – |
| Appendicularia | 0.6 | <0.1 | 0.6 | <0.1 | 4.7 | 0.5 | 2.0 | 0.1 | 3.6 | 11.7 | 3.1 | 0.8 |
| Telostei | | | | | | | | | | | | |
| Teleostei | | | | | – | – | – | – | 10.9 | 0.8 | 6.7 | 1.3 |
| Teleostei eggs | 4.9 | 0.4 | 4.2 | 0.3 | 1.5 | <0.1 | 1.4 | <0.1 | 1.4 | 20.7 | 1.5 | 0.5 |
| Teleostei scales | 1.5 | 0.2 | 1.0 | <0.1 | – | – | – | – | 0.7 | 0.2 | 0.7 | <0.1 |
| Diatoms | | | | | | | | | | | | |
| Pennate | 15.5 | – | – | | 71.4 | – | – | – | 18.2 | – | – | – |
| Centric | 6.7 | – | – | | 12.6 | – | – | – | 8.7 | – | – | – |
| Algae | | – | – | | – | – | – | – | 2.1 | – | 0.3 | – |

contributed to within-group similarities, according to SIMPER, were errant Polychaeta and Cyclopoida for *M. furnieri* and *D. rhombeus*, and errant Polychaeta and Calanoida for *E. argenteus*. No seasonal changes in diet were considered because no difference in diet composition among seasons was found according to a nonparametric Analysis of Similarity (ANOSIM).

Ontogenetic changes in diet

The diet composition of each size class showed that the diet of the largest individuals of the three species differed significantly from that of the smaller individuals. Three groups were formed by a cluster analysis based on the size classes of the three species (Fig. 1). In group I, errant Polychaeta was the food item consumed most by the two smaller size classes (≤40 mm TL) of *E. argenteus* and by the largest class (>40 mm TL) of *M. furnieri*. Calanoida was the second most important food item for *E. argenteus* in the smaller size class (group I, TL <30 mm). A second group (II) was formed by the two smallest classes of *M. furnieri* (≤40 mm TL) and *D. rhombeus* (≤40 mm TL), which had a diet based primarily on Cyclopoida and errant Polychaeta. The third group (III) was formed by the largest class

(>40 mm TL) of *E. argenteus* and *D. rhombeus*, which had a more varied diet in terms of the number of food items, primarily fish eggs (*E. argenteus*) and Nematoda (*D. rhombeus*) (Fig. 1).

Trophic strategy and niche breadth

The relative degree of individual specialisation in resource use, measured as the proportion of the total niche breadth of a population (TNB) explained by the within-individual component (WIC), indicates a specialist role for *M. furnieri* (WIC/TNB = 0.13) and *E. argenteus* (0.15) and a generalist role for *D. rhombeus* (0.78). Moreover, the total niche breadth of the population was larger for *E. argenteus* (TNB = 1.57) than for *M. furnieri* (TNB = 0.78) and *D. rhombeus* (TNB = 0.63).

Growth (in total length) was accompanied by increased niche breadth in the three species: *M. furnieri* (TL1 = 0.042, TL2 = 0.067 and TL3 = 0.074), *D. rhombeus* (TL1 = 0.220, TL2 = 0.222 and TL3 = 0.258), and *E. argenteus* (TL1 = 0.096, TL2 = 0.126 and TL3 = 0.133). Significant differences among niche breadth were found for *E. argenteus* ($H = 12.8$, $P = 0.002$) and *D. rhombeus* ($H = 20.5$, $P = 0.001$).
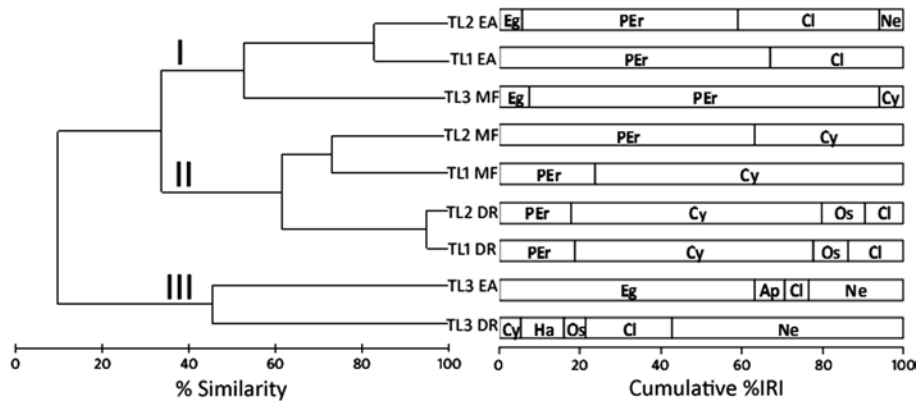
**Fig. 1** Cluster analysis of the size classes of *M. furnieri*, *D. rhombeus,* and *E. argenteus* based on the type and relative importance of their prey (%IRI), associated with the relative importance of the respective five main food items: Ha, Harpacticoida; Eg, Tel- eostei Eggs; PEr, errantia Polychaeta; PSe, sedentary Polychaeta; Cy, Cyclopoida; Cl, Calanoida; Sc, Teleostei Scales; Ne, Nematoda; Os, Ostracoda; Am, Amphipoda; My, Misydae; Bi, Bivalve; Lc, Crusta- cea Larvae; Si, Sipuncula; Fi, Fish; Ap, Appendicularia

**Table 3** Niche overlap index per size class (TL) for the three fish species (*M. furnieri,* MF; *D. rhombeus,* DR; and *E. argenteus,* EA) in a tidal mudflat in Sepetiba Bay

Values in bold indicate biologically significant overlap (>0.6) according to Labropoulou and Eleftheriou, [1997]

| Species size classes | *Micropogoniasfurnieri* | | | *Diapterus rhombeus* | | | *Eucinostomus argenteus* | | |
|---|---|---|---|---|---|---|---|---|---|
| | $TL1_{MF}$ | $TL2_{MF}$ | $TL3_{MF}$ | $TL1_{DR}$ | $TL2_{DR}$ | $TL3_{DR}$ | $TL1_{EA}$ | $TL2_{EA}$ | $TL3_{EA}$ |
| $TL1_{MF}$ | – | | | | | | | | |
| $TL2_{MF}$ | **0.93** | – | | | | | | | |
| $TL3_{MF}$ | 0.12 | 0.43 | – | | | | | | |
| $TL1_{DR}$ | **0.75** | **0.76** | 0.12 | – | | | | | |
| $TL2_{DR}$ | **0.90** | **0.91** | 0.17 | **0.94** | – | | | | |
| $TL3_{DR}$ | 0.07 | 0.07 | 0.01 | 0.37 | 0.24 | – | | | |
| $TL1_{EA}$ | 0.06 | 0.14 | 0.28 | 0.57 | 0.34 | 0.44 | – | | |
| $TL2_{EA}$ | 0.04 | 0.07 | 0.26 | 0.36 | 0.22 | **0.61** | 0.52 | – | |
| $TL3_{EA}$ | 0.01 | 0.01 | 0.05 | 0.58 | 0.31 | 0.54 | **0.83** | 0.52 | – |

Niche overlap

A high trophic overlap between species and size classes was not found, although a few pairwise comparisons indi- cated a very high degree of niche overlap (Table 3). The greatest amount of intraspecific overlap (>0.6) was found for the smallest size classes, as in *M. furnieri* ($TL1_{MF}$ versus $TL2_{MF}$ = 0.93) and *D. rhombeus* ($TL1_{DR}$ versus $TL2_{DR}$ = 0.94). *E. argenteus* showed a wider dietary over- lap among all size classes than the other species, primarily between $TL1_{EA}$ and $TL3_{EA}$ (0.83). Interspecific compari- sons showed that the highest overlap occurred between the two smallest size classes of *M. furnieri* and *D. rhombeus* due to the substantial contribution of Cyclopoida and Poly- chaeta (Table 3).

Prey/predator size ratio

The diet of *D. rhombeus* was composed primarily of prey less than 2 % of the predator's body size. In contrast, *E. argenteus* and *M. furnieri* incorporated a large number of

intermediate-sized prey in their diet. The sizes of these prey items ranged between 3 % and 6 % of the predators' body sizes (Fig. 2). The average trophic-niche breadth tended to decline with the increase in the prey size/predator size ratio for the three species investigated. The smallest size classes tended to have the lowest trophic-niche breadth and the highest prey size/predator size ratio, whereas the largest size classes tended to have the opposite pattern. The Caitipa mojarra *D. rhombeus* had the largest trophic-niche breadth and the smallest prey size/predator size ratio, whereas *M. furnieri* had the lowest trophic-niche breadth and the high- est prey size/predator size ratio (Fig. 2).

**Discussion**

A size-related shift in the diet was observed for the three species. The most conspicuous ontogenetic changes in the diet were recorded for *M. furnieri*, which shifted from a diet based on Cyclopoida, at smaller sizes, to Polychaeta as it attained a larger size. The gerreids, which used copepods
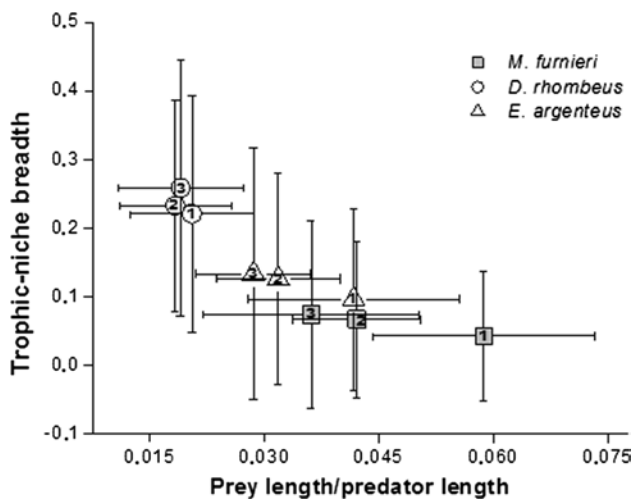
**Fig. 2** Average trophic-niche breadth plotted against prey size/predator size ratio. *Numbers* represent the size class: 1, Total Length$_1$ ≤30 mm; 2, TL$_2$ = 31–40 mm; and 3, TL$_3$ >40 mm. *Error bars*, ±1SD

and Polychaeta at the smaller sizes, shifted to a variety of items other than Polychaeta as they grew. The reason that conspecific individuals inhabiting a common environment would choose to use different subsets of the available resources remains relatively unknown. Cyclopoida usually swim in midwater, as opposed to the benthic errant Polychaeta associated with muddy bottoms (Brusca and Brusca 2002). Thus, when *M. furnieri* shifts its diet to errant Polychaeta, it most likely changes its foraging zone from mid-water to the bottom. *M. furnieri* undergoes several changes in morpho-meristic characteristics that are associated with changes in diet, such as shifts in mouth position and increase in the number of barbels and pores (sensory structures), characteristics that are functionally related to the ability to search for prey among the infauna. These changes in the diet indicate that there is a pattern of differential use of food resources among different size classes of *M. furnieri* and suggest a possible ecological strategy to reduce intraspecific competition for food within the population (Schoener 1974).

The absence of Polychaeta in the diet of the largest size classes of the gerreids contrasts with the abundance of this food item in the largest size classes of *M. furnieri*, which appear to be well adapted to exploit this feeding resource. Gerreids intensely inspect the substrate, a behaviour pattern that indicates that they depend on vision to locate prey, whereas *M. furnieri* apparently touch the substrate with their barbels to find prey (Hobson and Chess 1986). Important changes in feeding habits for species in the family Gerreidae are associated with mouth protractibility and increase in the size of the eyes during growth, factors that are important for the success in locating and acquiring food

(Kerschner et al. 1985). Cyrus and Blaber (1983) suggest that changes in mouth structure facilitate the rapid protractibility of the jaws and increase the probability of prey capture. Visual capacity supports the ability to attack prey in turbid waters (Zahorcsak et al. 2000). Furthermore, dietary changes can be related to intra- and interspecific behaviour, such as territorial responses to maintain control of sites where food occurs. Alternatively, dietary changes can be related to variation in resource availability (Muñoz and Ojeda 1998).

Individual specialisation in resource use was found for *M. furnieri* and *E. argenteus*. This specialisation was accompanied by a high between-individual contribution (BPC) to the niche breadth of these two species. In contrast, *D. rhombeus* was found to be a resource generalist, with a high within-individual contribution (WPC) to niche breadth. The broadest population niche breadth was found for *E. argenteus*, whereas the narrowest was found for *D. rhombeus*. The broad population niche breadth for *E. argenteus* is associated with an increase in the BPC. New prey types are incorporated in the diet as *E. argenteus* attains larger sizes. Van Valen (1965) proposed that in the absence of interspecific competition, niche expansion was achieved through an increased BPC in resource use. The BPC represents only a small fraction of the population niche breadth if individuals are specialised to use a specific region of the resource axis (Roughgarden 1972).

Overall, niche breadth was greater for the largest than for the smallest juveniles, especially for *M. furnieri* and *E. argenteus*. Such ontogenetic changes in diet have been reported for many fish species (Cabral 2000; Gning et al. 2010). These changes are generally associated with fish movements within the area covered by the distribution of the organisms and to changes in morphological structures associated with search and prey capture. Foraging theory suggests that by decreasing the frequency of preferred prey, resource competition should increase the diet breadth of the population (Schoener 1971; Stephens and Krebs 1986). This increase should occur if different phenotypes resort to different alternative prey. As prey density declines, the phenotypes increasingly rely on different resources. However, the proximate and ultimate causes of this among-individual variation remain poorly understood.

The trophic strategy differed among the three species investigated. Individuals of *M. furnieri* larger than 20 mm TL tended to specialise on Polychaeta, whereas the larger individuals (TL larger than 40 mm) of *E. argenteus* behaved as trophic generalists. Moreover, *D. rhombeus* had a more pronounced generalist strategy in all size classes, with high values for WPC. The tendency to specialisation can reflect changes in feeding habits resulting from individual foraging specialisations that produce changes in the BPC caused by changes in the available resource. This strategy serves

to maximise the benefits represented by energy gains (Bolnick et al. 2002, 2003). In contrast, the development of a generalist strategy (e.g., *D. rhombeus* in all size classes and *E. argenteus* larger than 40 mm TL) enables individuals to be potentially capable of using a given resource, even if the intensity of use of the resource is low, compared with fishes that show a specialist strategy. Such a generalist strategy was developed as a way to decrease intraspecific competition because an increase in niche breadth by a given species is a means of avoiding exploitation competition (Wootton 1990). Svanbäck and Bolnick (2007) reported that resource competition can produce increased dietary variation among the members of a single population. Because intraspecific competition is generally considered strong and widespread (Gurevitch et al. 1992), the dynamics documented here may play a major role in maintaining ecological variation within populations. Moreover, such resource partitioning among size classes provides an understanding of species interactions and resource use.

There is an inverse relationship between the niche breadth and the relative prey size, with the range of relative sizes of prey eaten expanding with increasing predator body size. The three species investigated primarily consumed prey that were a small fraction of their own body size. Differential size-based feeding strategies were evident for the examined species, as the predator diets were concentrated on varying ranges of relative prey sizes. The prey ranged from 1 to 2 % of the predator's size (*D. rhombeus*) to between 3 and 7 % of the predator's size (*E. argenteus* and *M. furnieri*). These findings contrast with the patterns reported by Scharf et al. (2000) for marine fish predators from the continental shelf waters off the coast of the northeastern USA, where trophic-niche breadths generally did not expand during predator ontogeny and tended to become narrower for the largest predators. The findings for the three species examined in this study provide further evidence for the potential importance of factors other than predator gape size, such as behaviour, prey availability, and predator capture efficiency, in limiting maximum prey size.

The primary goal of resource partitioning studies is to describe the limits that interspecific competition places on the number of species that may stably coexist (Schoener 1974; Ross 1986). The dietary overlap among size classes for each species was lower than the dietary overlap of species pairs within a given size class. A pattern of "size-structured components" of niche partitioning was identified. This pattern suggests that stabilizing coexistence is present because there is selective pressure for size groups to diverge in resource use under conditions of reduced interspecific competition. The implications of these ontogenetic dietary shifts appear to be of substantial importance for avoiding intra- and interspecific competition. The inclusion of more life history stages in future studies will be important for having a more holistic understanding of resource partitioning in mudflat areas.

## References

Araújo FG, Santos ACA (1999) Distribution and recruitment of mojarras (Perciformes, Gerreidae) in the continental margin of Sepetiba Bay, Brazil. Bull Mar Sci 65:431–439

Araújo FG, Azevedo MCC, Silva MA, Pessanha ALM, Gomes ID, Cruz-Filho AG (2002) Environmental influences on the demersal fish assemblages in the Sepetiba Bay, Brazil. Estuaries 25:441–450

Bolnick DI, Yang LH, Fordyce JA, Davis JM, Svanback R (2002) Measuring individual-level resource specialization. Ecology 83:2936–2941

Bolnick DI, Svanback R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, Forister ML (2003) The ecology of individuals: incidence and implications of individual specialization. Am Nat 161:1–28

Brusca RC, Brusca GJ (2002) Invertebrates, 2nd edn. Sinauer Associates, Sunderland

Cabral HN (2000) Comparative feeding ecology of sympatric *Solea solea* and *S. senegalensis*, within the nursery areas of the Tagus estuary, Portugal. J Fish Biol 57:1550–1562

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Aust J Ecol 18:117–143

Costa MR, Araújo FG (2003) Use of a tropical bay in Southeastern Brazil by juvenile and subadult *Micropogonias furnieri* (Perciformes, Sciaenidae). ICES J Mar Sci 60:268–277

Cyrus DP, Blaber SJM (1983) Diet of *Gerres* fry in the Kosi system. S Afr J Zool 18:403–406

Degre D, Leguerrier D, Armynot du Chatelet E, Rzeznik J, Auguet J, Dupuy J, Marquis E, Fichet D, Struski D, Joyeux D, Sauriau P, Niquil N (2006) Comparative analysis of the food webs of two intertidal mudflats during two seasons using inverse modelling: Aiguillon Cove and Brouage Mudflat, France. Estuar Coast Shelf Sci 69:107–124

Florin A, Lavados G (2010) Feeding habits of juvenile flatfish in relation to habitat characteristics in the Baltic Sea. Estuar Coast Shelf Sci 86:607–612

Gning G, Loc'h F, Thiawc OT, Aliaume C, Vidy G (2010) Estuarine resources use by juvenile Flagfin mojarra (*Eucinostomus melanopterus*) in an inverse tropical estuary (Sine Saloum, Senegal). Estuar Coast Shelf Sci 86:683–691

Guedes APP, Araujo FG (2008) Trophic resource partitioning among five flatfish species (Actinopterygii, Pleuronectiformes) in a tropical bay in south-eastern Brazil. J Fish Biol 72:1035–1054

Gurevitch J, Morrow LL, Wallace A, Walsh JS (1992) A meta-analysis of competition in field experiments. Am Nat 140:539–572

Hajisamae S (2009) Trophic ecology of bottom fishes assemblage along coastal areas of Thailand. Estuar Coast Shelf Sci 82:503–514

Hajisamae S, Chou LM, Ibrahim S (2003) Feeding habits and trophic organization of the fishes community in shallow waters of a impacted tropical habitat. Estuar Coast Shelf Sci 58:89–98

Hobson ES, Chess JR (1986) Relationships among fishes and their prey in a nearshore sand community of southern California. Environ Biol Fish 17:201–226

Holbrook SJ, Schmitt RJ (1992) Causes and consequences of dietary specialization in surf perches, patch choice and intra-specific competition. Ecology 73:402–412

Hourston M, Platell ME, Valensini FJ, Potter IC (2004) Factors influencing the diets of four morphologically divergent fish species in nearshore marine waters. J Mar Biol Assoc UK 84:805–817

Hyslop EJ (1980) Stomach contents analysis—a review of methods and their application. J Fish Biol 17:411–429

Kanou K, Sano M, Kohno H (2004) Food habits of fishes on unvegetated tidal mudflats in Tokyo Bay, central Japan. Fish Sci 70:978–987

Kerschner BA, Peterson MS, Gilmore RG (1985) Ecotopic and ontogenetic trophic variations in mojarras (Pisces: Gerreidae). Estuaries 8:311–322

Krebs CJ (1989) Ecological methodology. Harper and Row Publishers, New York

Labropoulou M, Eleftheriou A (1997) The foraging ecology of two pairs of congeneric demersal fish species: importance of morphological characteristics in prey selection. J Fish Biol 50:324–340

Meng L, Powell JC (2003) Linking juvenile fish and their habitats: an example from Narragansett Bay, Rhode Island. Estuaries 22:905–916

Mittelbach GG, Osenberg CW, Leibold MA (1988) Trophic relations and ontogenetic niche shifts in aquatic ecosystems. In: Ebenman B, Persson L (eds) Size-structured populations. Springer, Berlin, pp 219–235

Muñoz AA, Ojeda FP (1998) Guild structure of carnivorous intertidal of the Chilean coast: implications of ontogenetic dietary shifts. Oecologia 114:563–573

Ojeda FP, Dearborn JH (1991) Feeding ecology of benthic mobile predators: experimental analysis of their influence in rocky subtidal communities of the Gulf of Maine. J Exp Mar Biol Ecol 149:13–44

Olson MH (1996) Ontogenetic niche shifts in largemouth bass: variability and consequences for first-year growth. Ecology 77:179–190

Olson MH, Mittelbach GG, Osenberg CW (1995) Competition between predator and prey: resource-based mechanisms and implications for stage-structured dynamics. Ecology 76:1758–1771

Osenberg CW, Mittelbach GG, Wainwright PC (1992) Two-stage life histories in fish: the interaction between juvenile competition and adult performance. Ecology 73:255–267

Paterson AW, Whitfield AK (2000) Do shallow-water habitats function as refugia for juvenile fishes? Estuar Coast Shelf Sci 51:359–364

Pessanha ALM, Araújo FG (2003) Spatial, temporal and diel variations of fish assemblage at two sandy beaches in the Sepetiba Bay, Rio de Janeiro, Brazil. Estuar Coast Shelf Sci 57:817–828

Pessanha ALM, Araújo FG, Azevedo MCC, Gomes ID (2003) Diel and seasonal changes in the distribution of fish on a southeast Brazil sandy beach. Mar Biol 143:1047–1055

Pinkas L, Oliphant MS, Iverson ILK (1971) Food habits of albacore, bluefin tuna and bonito in California waters. Calif Fish Game 152:1–105

Platell ME, Potter IC (2001) Partitioning of food resources amongst 18 abundant benthic carnivorous fish species in marine waters on the lower west coast of Australia. J Exp Mar Biol Ecol 261:31–54

Ross ST (1978) Trophic ontogeny of the leopard searobin, *Prionotus scitulus* (Pisces: Triglidae). Fish Bull NOAA 76:225–234

Ross ST (1986) Resource partitioning in fish assemblages: a review of field studies. Copeia 1986:352–388

Roughgarden J (1972) Evolution of niche width. Am Nat 106:683–718

Schafer LN, Platell ME, Valesini FJ, Potter IC (2002) Comparisons between the influence of habitat type, season and body size on the dietary compositions of fish species in nearshore marine waters. J Exp Mar Biol Ecol 278:67–92

Scharf FS, Juanes F, Rountree RA (2000) Predator size—prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. Mar Ecol Prog Ser 208:229–248

Schmitt RJ, Coyer JA (1982) The foraging ecology of sympatric marine fish in the genus Embiotoca (Embiotocidae): importance of foraging behavior in prey size selection. Oecologia 55:369–378

Schoener TW (1971) Theory of feeding strategies. Annu Rev Ecol Syst 2:369–404

Schoener TW (1974) Resource partitioning in ecological communities. Science 185:27–39

Signorini SR (1980) A study of the circulation in bay of Ilha Grande and bay of Sepetiba, Part I. A survey of the circulation based on experimental field data. Bol Inst Ocean 29:41–55

Stephens DW, Krebs JR (1986) Foraging theory. Princeton University Press, Princeton

Svanbäck R, Bolnick D (2007) Intraspecific competition drives increased resource use diversity within a natural population. P Roy Soc Lond B Biol 274:839–844

Taper ML, Case TJ (1985) Quantitative genetic models for the coevolution of character displacement. Ecology 66:355–371

Uiblein F (1991) Food searching decisions in four cyprinid species. Environ Biol Fish 33:47–52

Van Valen L (1965) Morphological variation and the width of ecological niche. Am Nat 99:377–389

Vicentini RN, Araújo FG (2003) Sex ratio and size structure of *Micropogonias furnieri* (Desmarest) (Pisces: Sciaenidae) in the Sepetiba Bay, Rio de Janeiro, Brazil. Braz J Biol 63:559–566

Vinagre C, França S, Cabral NH (2006) Diel and semi-lunar patterns in the use of an intertidal mudflat by juveniles of Senegal sole, *Solea senegalensis*. Estuar Coast Shelf Sci 69:246–254

Werner EE, Gilliam JF (1984) The ontogenetic niche and species interactions in size structured populations. Annu Rev Ecol Syst 15:393–425

Wootton RJ (1990) Ecology of teleost fishes. Chapman and Hall, London

Zahorcsak P, Silvano RAM, Sazima I (2000) Feeding biology of a guild of benthivorous fishes in a sandy shore on the south-eastern Brazilian coast. Rev Bras Biol 60:510–511