

## Trophic resource partitioning among five flatfish species (Actinopterygii, Pleuronectiformes) in a tropical bay in south-eastern Brazil

A. P. P. GUEDES AND F. G. ARAÚJO\*

*Universidade Federal Rural do Rio de Janeiro, Laboratório de Ecologia de Peixes, Km 47, Antiga Rodovia Rio – São Paulo, 23851-970, Seropédica, RJ, Brazil*

(Received 13 February 2007, Accepted 22 November 2007)

Five species of flatfishes in a tropical bay in south-eastern Brazil were studied to test the hypothesis that resource partitioning along the spatial and size dimensions has been used as a mechanism to enable coexistence. Three zones in the study area were defined according to environmental characteristics (inner, middle and outer). Sampling was conducted by otter trawl tows during daylight hours, between October 1998 and September 1999. Achiridae species (*Achirus lineatus* and *Trinectes paulistanus*) showed narrow niche width, indicating a specialized feeding strategy, preying on Polychaeta, and occurring mainly in the inner bay zone. Paralichthyidae (*Citharichthys spilopterus* and *Etropus crossotus*) and the Cynoglossidae (*Symphurus tessellatus*) showed broad niche width and a generalized feeding strategy preying on a large number of Crustacea. *Symphurus tessellatus* did not change diet with size-dimension feeding on Amphipoda and Polychaeta, whereas *C. spilopterus* and *E. crossotus* shifted diet with growth. *Citharichthys spilopterus* fed mainly on Mysida and secondarily on shrimps, with juvenile preying on large amounts of Calanoida, whereas adults consumed large amounts of fishes. Isaeidae amphipods were a significant prey for both small and large *E. crossotus*, whereas Polychaeta Errantia were used mainly by large fishes. *Etropus crossotus* and *S. tessellatus* share similar feeding resources in outer bay zone preying on Isaeidae and Polychaeta Errantia. Differences in the Pleuronectiformes diet composition along with spatial and size changes in the use of the available resources contributed to allow the organisms' coexistence in Sepetiba Bay. The high item diversity used by flatfishes indicates that the system plays an important role as a feeding ground, and that interspecific competition for food was unlikely.

© 2008 The Authors

Journal compilation © 2008 The Fisheries Society of the British Isles

Key words: bays; competition; demersal fishes; diet; partitioning resources.

### INTRODUCTION

Resource partitioning has been used by fish species to avoid inter- and intra-specific competition, influencing the number of individuals that can coexist in the same area. According to Schoener (1974), resource partitioning may occur

\*Author to whom correspondence should be addressed. Tel.: +55 21 94541989; fax: +55 21 37873983; email: [gerson@ufrj.br](mailto:gerson@ufrj.br)

by segregation with one of the three main resource axes: food, space and time. Ross (1986) reported that trophic separation explains most of the co-existence mechanisms among closely related species. Food is probably one of the most important factors determining habitat quality, and food abundance can affect distribution patterns. The site occupied by an individual is presumably selected in response to factors that optimize its net energy gain while avoiding predators (Baltz & Jones, 2003). Furthermore, comparative studies of partitioning of habitat can provide insights into the interaction between species.

Flatfishes are predators, normally associated with the substratum, reflecting their benthic feeding habits and the ability to bury themselves (Gibson & Robb, 1992). They have the capacity to camouflage as a tactic to catch their prey, or to escape predation (Gibson, 2005). With their similarity in body shape and distinct preference for the benthic layer, flatfishes may be more similar in their habits and environmental demands than any other fishes (Piet *et al.*, 1998), and competitive interactions may be a dominant feature shaping the flatfish assemblage.

Prey items in the benthic community vary widely, as seen in the diverse diet composition of flatfishes in different areas. Functionally similar and preferred prey are generally selected by the fact that the differences in the availability of these prey result in differing diets (Gibson, 2005). A fish may have to choose between a habitat that provides more abundant and diverse prey, but in which the prey is harder to capture, and a habitat which has less prey, but better capture opportunity. In semi-closed embayment areas, increased nutrient levels could change natural conditions modifying local nursery habitats for flatfishes (Allen & Baltz, 1997). Some species can develop the ability to use resources and can exist in the higher stress conditions in inner bay zones, while others may be more limited to the stable condition of outer bay zones.

Ontogenetic changes in feeding habits are actually adaptations to use available food, avoiding intra and interspecific competition, and to enable the catching of larger and more energetic prey (Beyst *et al.*, 1999; Amara *et al.*, 2001; Amezcua *et al.*, 2003). All flatfishes eat polychaetes and small benthic crustaceans at some period in their life history. Many of the piscivores and specialists consume polychaetes and meiofauna when they are of smaller sizes, but grow out of this feeding mode (Toepfer & Fleeger, 1995; Aarnio *et al.*, 1996; Garrison & Link, 2000). There are few references on ontogenetic changes in flatfishes in the tropical bays where several species recruit and spend part of their life cycle. Understanding this aspect of life history is a very important step to enhance the knowledge of the ecology of flatfishes.

Sepetiba Bay has suffered from human impacts that originate from the outskirts of Rio de Janeiro State, and a few medium-sized towns that have limited agriculture and fishing, in addition to increasing industrial development. Recent enhancement of Sepetiba Port included dredging of the access channel to 20 m depth, which enables it to receive ships up to 150 000 t (Araújo *et al.*, 2002). The aim of this work was to describe the diet of the five most abundant flatfishes in Sepetiba Bay, and to test the hypothesis that resource partitioning along the spatial and size dimensions has been used by these species as a mechanism to allow coexistence.

## MATERIALS AND METHODS

### STUDY AREA AND SAMPLING

Sepetiba Bay (22°54'–23°04' S; 43°34'–44°10' W) is a sedimentary embayment located in Rio de Janeiro State, south-eastern Brazil, with an area of 520 km<sup>2</sup> encompassing a wide range of habitats, including mangroves, sandbanks and small estuarine areas. The overall depth is <5 m, and the waters are rich in organic nutrients from continental drainage; the bottom is predominantly muddy. The bay plays an important role in regional aquatic ecology, mainly for juvenile fishes that use the area as a nursery ground (Vicentini & Araújo, 2003).

The bay was divided into three zones according to depth, salinity gradient and human influences (Azevedo *et al.*, 2006) (Fig. 1). The inner zone is influenced by discharges from perennial small rivers with increased turbidity and temperature and decreased salinity; the substratum is mainly muddy, with depths mostly <5 m, and a salinity averaging 28. This zone is the most altered because of the increasing industrial development nearby (Leal Neto *et al.*, 2006). The outer zone near the sea, presents contrasting environmental conditions: substratum mainly sandy, comparatively lower temperature and higher salinity and transparency; maximum depth is *c.* 28 m, and salinity averages 33. The middle zone presents intermediate environmental conditions between inner and outer zones.

Fishes were sampled by monthly otter trawling during daylight hours between October 1998 and September 1999. In each zone, three replicate samples were taken. Tows were against the current, of 30 min duration at the bottom, at a towing speed of *c.* 3 km h<sup>-1</sup> and covering a distance of 1500 m. The trawl had an 8 m headline, 11 m ground rope, 25 mm stretched mesh and 12 mm mesh codend liner. The bottom depth in the areas trawled ranged from 4 to 25 m.

Immediately after collection, fishes were anaesthetized in benzocaine hydrochloride (50 mg l<sup>-1</sup>), and then fixed in 10% formaldehyde–seawater solution. After 48 h, they were transferred to 70% ethanol. All flatfishes were identified according to Munroe (1998) and Figueiredo & Menezes (2000), and measured to the nearest mm standard

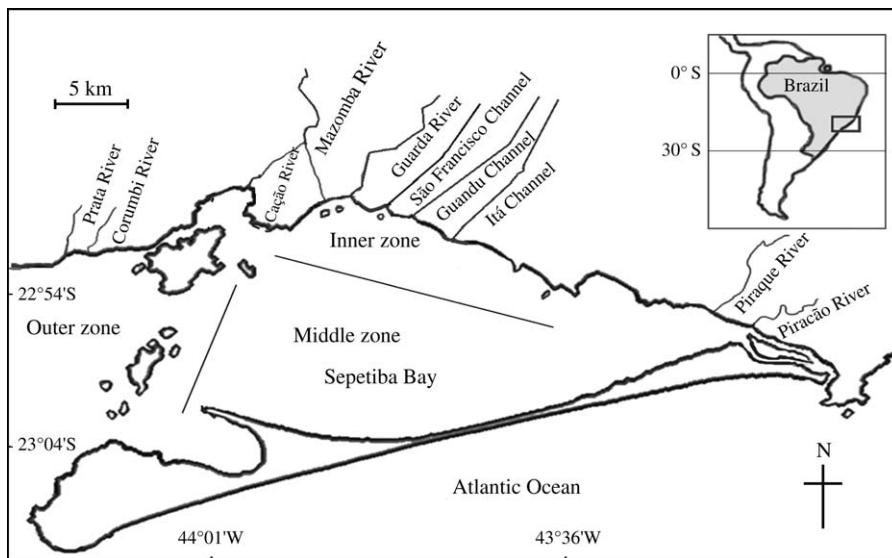


FIG. 1. Map showing the three zones (outer, middle and inner) of Sepetiba Bay, Brazil.

length ( $L_S$ ). Stomachs were removed and food items were identified to the lowest possible taxonomic level.

## DATA ANALYSIS

Stomach contents of flatfishes were analysed from a sub-sample of the flatfishes captured in each zone. If a sample consisted of <15 flatfish of each species, all stomachs were dissected and examined. In samples of >15 fish of a species, 15 individuals covering a wide size range from each zone in each month were selected for dissection. Empty stomachs or those with unidentifiable contents were excluded from the analyses.

Food composition was expressed for each food item as a percentage of index of relative importance ( $I_{RI}$ ) developed by Pinkas *et al.* (1971), which described the relative contribution of food items in the diet as the calculation of the frequency of occurrence (% $F_O$ ) and percentage composition by number (% $N$ ) and by mass (% $M$ ) (Berg, 1979; Hyslop, 1980; Clark, 1985). The  $I_{RI}$  enables comparisons among studies and gives a robust estimate of relative importance of the prey by depicting all three single measurements graphically to visualize the importance of each food category. The  $I_{RI}$  was calculated using the equation:  $I_{RI} = (%N + \%M) \times \%F_O$ . It was expressed on a per cent basis, such that % $I_{RI}$  for a specific food category  $i$  ( $I_{RIi}$ ) becomes:  $\%I_{RIi} = 100I_{RIi} / (\sum_{i=1}^n I_{RIi})^{-1}$ , where  $n$  is the total number of food categories considered at a given taxonomic level (Cortès, 1997).

Trophic strategy was described according to the Amundsen graphical method (Amundsen *et al.*, 1996). The food items were expressed as the percentage composition of prey-specific % $M$  in fishes that contained that food item and % $F_O$ . The % $F_O$  was plotted against % $M$ , and then interpreted with respect to the position within the graph. The trophic niche width and the homogeneity of items distribution were determined using the Shannon–Wiener  $H'$  and the evenness  $J'$  indices, respectively (Krebs, 1989). Cluster analysis on mode Q, using the City-block distance and Ward method, was used to detect patterns in diet. The matrix in cluster analysis was constructed from the  $I_{RI}$  values at the various species representing habitat type (bay zones) and  $L_S$  classes. A one-way ANOVA was used to ascertain whether food items differed significantly among the groups formed by cluster analysis ( $P < 0.05$ ). Tukey's multiple range test was used to determine differences in mean values following ANOVA (Zar, 1999).

Diet overlap was calculated by the simplified Morisita's index (Krebs, 1989). 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 & Eleftheriou (1997) suggested that values >0.6 should be considered as biologically significant.

Spatial comparisons were performed considering the three bay zones (inner, middle and outer). Flatfishes were assigned to three  $L_S$  classes ( $L_{S1}$ ,  $L_{S2}$  and  $L_{S3}$ ) to evaluate size-related patterns of resource use: *Citharichthys spilopterus* Günther ( $L_{S1} < 71$  mm;  $L_{S2} = 71$ –100 mm;  $L_{S3} > 100$  mm), *Etropus crossotus* Jordan & Gilbert ( $L_{S1} < 80$  mm;  $L_{S2} = 80$ –100 mm;  $L_{S3} > 100$  mm) and *Symphurus tessellatus* (Quoy & Gaimard) ( $L_{S1} < 105$  mm;  $L_{S2} = 105$ –140 mm;  $L_{S3} > 140$  mm). These size classes were defined according to the size at first maturation (intermediate class) for each species (Munroe, 1998; Reichert, 1998; Castillo-Rivera *et al.*, 2000). Therefore, it was assumed that  $L_{S1}$  corresponds to juveniles,  $L_{S2}$  to subadults and  $L_{S3}$  to adults. Spatial and size comparisons were not performed for *Achirus lineatus* (L.) and *Trinectes paulistanus* (Ribeiro) owing to the low number of individuals.

## RESULTS

### SPECIES OCCURRENCE

*Achirus lineatus* occurred mainly in the inner and middle zones, while *T. paulistanus* occurred almost exclusively in the inner zone. On the other hand, *C. spilopterus*,

*E. crossotus* and *S. tessellatus* were widespread in all three bay zones. *Etropus crossotus* and *S. tessellatus* were more abundant in the outer zone (Table I).

### TROPHIC STRATEGY AND TROPHIC NICHE WIDTH

Species of Achiridae (*A. lineatus* and *T. paulistanus*) showed a specialized feeding strategy according to the Amundsen diagram, preying basically on Polychaeta Errantia. Other items were occasionally found in the stomach contents, reflecting the narrow niche width for these species. Species of Paralichthyidae (*C. spilopterus* and *E. crossotus*) and the Cynoglossidae (*S. tessellatus*) appeared to mark a transition towards a more generalized feeding strategy and exhibited a broad dietary niche width. The most frequent food item in *C. spilopterus* was Mysida (>50%), whereas in *E. crossotus* it was Isaeidae amphipods, Polychaeta Errantia and Isopoda, all of them with  $F_O > 50\%$ . The dominant food items in *S. tessellatus* were Isaeidae (59.7%  $F_O$ ; 23.0%  $M$ ) and Polychaeta Errantia (31.3%  $F_O$ ; 71.1%  $M$ ) (Fig. 2).

Achiridae species showed narrow niche width according to the Shannon–Wiener index ( $H'$ ) and lower evenness (Table II). Although *C. spilopterus* preyed on a higher diversity of food items (26), it did not show the broadest dietary niche width among the studied species ( $H' = 0.21$ ;  $J' = 0.35$ ). *Etropus crossotus* showed the broadest niche width ( $H' = 0.33$ ) and the largest evenness ( $J' = 0.57$ ), suggesting feeding plasticity and the ability to use available resources. *Symphurus tessellatus* showed a narrow dietary niche width and evenness when compared with *E. crossotus* and *C. spilopterus*.

### RESOURCE PARTITIONING

Cluster analysis on the  $I_{RI}$  of the five flatfishes showed three groups (Fig. 3). Group 1 consisted of *E. crossotus* and *S. tessellatus* (Crustacea eaters). Group 2 was formed by *C. spilopterus* (Crustacea and Teleostei eaters) and group 3 comprised *A. lineatus* and *T. paulistanus* (Polychaeta eaters).

TABLE I. Number of captured and examined (in parentheses) individuals in Sepetiba Bay zones (see Fig. 1), 1998–1999

Species	Zones			Total
	Inner	Middle	Outer	
<i>Achirus lineatus</i>	27 (21)	14 (14)	3 (3)	44 (38)
<i>Trinectes paulistanus</i>	223 (54)	9 (9)	1 (1)	233 (64)
<i>Citharichthys spilopterus</i>	88 (83)	77 (72)	40 (40)	205 (195)
<i>Etropus crossotus</i>	113 (43)	186 (121)	641 (141)	940 (305)
<i>Symphurus tessellatus</i>	73 (70)	61 (54)	128 (123)	262 (247)
Total number	524 (271)	347 (270)	813 (308)	1684 (849)

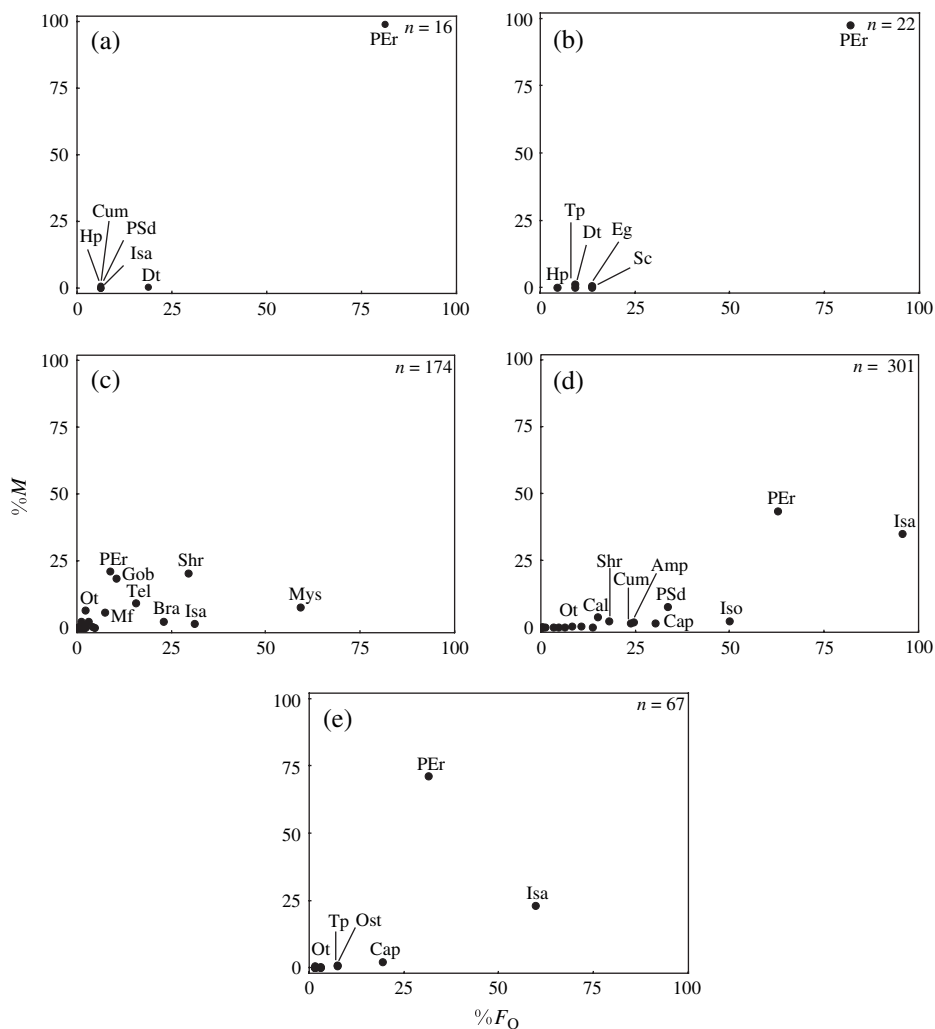


FIG. 2. Feeding strategy plots for flatfish species in Sepetiba Bay, Brazil (a) *Achirus lineatus*, (b) *Trinectes paulistanus*, (c) *Citharichthys spilopterus*, (d) *Etropus crossotus* and (e) *Symphurus tessellatus*. *n*, number of fish examined with food in the stomach. Food items identified as: Amp, Ampeliscidae; Bra, Brachyura; Cal, Calanoida; Cap, Caprellidae; Cum, Cumacea; Dt, Diatomacea; Eg, eggs; Gob, Gobiidae; Hp, Harpacticoida; Isa, Isaeidae; Iso, Isopoda; Mf, *Micropogonias furnieri*; Mys, Mysida; Ost, Ostracoda; Ot, others; PEr, Polychaeta Errantia; PSd, Polychaeta Sedentaria; Sc, scales; Shr, unidentified shrimps; Tel, unidentified Teleostei; Tp, tube of Polychaeta.

### Spatial variation

Polychaeta Errantia was the dominant food item for all species in the inner zone, except in *E. crossotus*, which ate mainly Isaeidae amphipods (55.77%  $I_{RI}$ ) and Polychaeta Sedentaria (25.82%  $I_{RI}$ ). In the middle and outer zones, Polychaeta Errantia and Isaeidae were the dominant items in *S. tessellatus* and *E. crossotus*, while Mysida was the main food item in *C. spilopterus* (Table III).

Cluster analysis on the % $I_{RI}$  food items for the three species in bay zones (inner, middle and outer) showed two feeding groups (Fig. 4). Group 1 formed

TABLE II. Mean  $\pm$  s.e. for Shannon–Weiner index ( $H'$ ) and evenness ( $J'$ ) for five flatfish species in Sepetiba Bay, Brazil

Species	$n$	$H'$	$J'$
<i>Achirus lineatus</i>	6	0.05 $\pm$ 0.03	0.16 $\pm$ 0.09
<i>Trinectes paulistanus</i>	6	0.05 $\pm$ 0.02	0.14 $\pm$ 0.07
<i>Citharichthys spilopterus</i>	26	0.21 $\pm$ 0.01	0.35 $\pm$ 0.02
<i>Etropus crossotus</i>	20	0.33 $\pm$ 0.01	0.57 $\pm$ 0.01
<i>Symphurus tessellatus</i>	14	0.10 $\pm$ 0.02	0.29 $\pm$ 0.05

$n$ , number of food items.

by *E. crossotus* and *S. tessellatus* (all three zones), showed significantly ( $P < 0.05$ ) higher values for Crustacea Isaeidae, and group 2 composed of *C. spilopterus* only (all three zones), which showed the highest % $I_{RI}$  values for Crustacea (Mysida, Sergestidae and unidentified shrimps) and Teleostei (Table IV).

#### Size variation

Mysida was the main item in all  $L_S$  classes for *C. spilopterus*, followed by Calanoida (21.09%  $I_{RI}$ ) in the smallest individuals (juveniles), unidentified shrimps (9.68%  $I_{RI}$ ) in subadults and Isaeidae (22.71%  $I_{RI}$ ) in adults. Isaeidae was the main item for all  $L_S$  classes in *E. crossotus* and *S. tessellatus*, followed by Polychaeta Errantia for subadults and adults. Differences in the use of secondary items between these two species were found in juveniles, with *E. crossotus* preying mainly on Calanoida (14.48%  $I_{RI}$ ) and *S. tessellatus*, preying mainly on Caprellidae (13.71%  $I_{RI}$ ) (Table V).

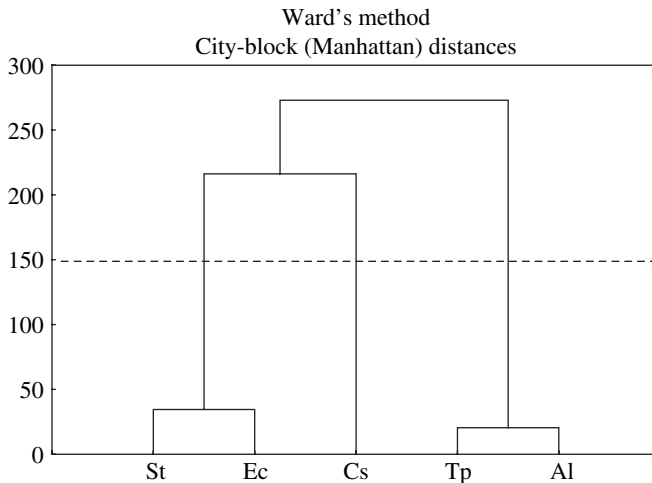


FIG. 3. Dendrogram resulting from the cluster analysis performed on stomach contents data (per cent index of relative importance) of five flatfish species (Al, *Achirus lineatus*; Cs, *Citharichthys spilopterus*; Ec, *Etropus crossotus*; St, *Symphurus tessellatus*; Tp, *Trinectes paulistanus*) of Sepetiba Bay.

TABLE III. Index of relative importance (% $I_{RI}$ ) for food items of flatfish species [*Citharichthys spilopterus* (Cs), *Etropus crossotus* (Ec) and *Symphurus tessellatus* (St)] in three zones of Sepetiba Bay

Trophic category	Food Items	Inner zone			Middle zone			Outer zone			All zones		
		Cs	Ec	St	Cs	Ec	St	Cs	Ec	St	Cs	Ec	St
Polychaeta	Polychaeta Sedentaria	—	25.82	—	—	2.83	—	—	0.41	0.01	—	3.04	0.01
	Polychaeta Errantia	24.64	7.99	60.19	0.01	23.86	42.35	0.01	23.35	25.34	—	24.50	28.97
Crustacea	Tube of Polychaeta	—	—	—	—	—	—	—	—	0.45	—	—	0.37
	Decapoda	—	—	—	—	—	—	—	—	—	—	—	—
	Penaidae	—	—	—	—	—	—	0.62	—	—	—	0.06	—
	Sergestidae	—	—	—	0.03	—	—	0.02	—	—	—	0.01	—
	Ogyrididae	—	—	—	—	—	—	0.01	—	—	—	<0.01	—
	Shrimps n.i.	14.24	0.56	—	11.31	0.24	—	13.52	0.35	—	—	15.81	0.38
	Brachyura larvae	<0.01	0.23	—	0.08	0.06	15.27	0.02	<0.01	—	—	0.03	0.04
	Brachyura	0.76	0.01	—	0.35	0.02	—	15.97	0.05	—	—	3.48	0.03
	Anomura	—	—	—	—	<0.01	—	—	—	—	—	—	<0.01
	Mysida	19.85	<0.01	—	67.99	0.01	—	65.47	<0.01	—	—	54.74	0.01
	Cumacea	—	—	—	—	1.21	—	—	0.37	—	—	—	0.54
	Tanaidacea	—	—	3.59	—	<0.01	—	—	—	0.01	—	—	<0.01
	Isopoda	—	9.07	—	0.15	18.58	—	—	0.75	0.01	—	0.02	8.05
	Amphipoda	—	—	—	—	—	—	—	—	—	—	—	—
Isaetidae	6.77	55.77	30.21	9.55	32.81	42.38	3.14	72.97	71.81	—	7.60	57.30	
Ampeliscidae	—	0.01	—	—	0.11	—	—	1.34	—	—	—	0.60	
Platyschnopsidae	—	—	—	—	—	—	—	—	0.02	—	—	—	
Liljeborgiidae	—	<0.01	—	—	<0.01	—	—	<0.01	—	—	—	<0.01	
Caprellidae	<0.01	0.21	4.05	0.27	2.09	—	0.07	0.36	2.06	—	0.09	0.85	
Copepoda	—	—	—	—	—	—	—	—	—	—	—	—	
Calanoida	15.79	0.03	1.97	0.04	18.14	—	—	<0.01	—	—	3.13	4.60	
Cyclopoida	—	—	—	—	<0.01	—	—	—	—	—	—	<0.01	
Harpacticoida	—	<0.01	—	—	0.01	—	—	—	—	—	—	<0.01	
Ostracoda	0.36	0.10	—	—	0.02	—	—	<0.01	0.24	—	0.06	0.01	
Crustacea fragments	—	—	—	—	—	—	—	—	0.01	—	—	—	



TABLE III. Continued

Trophic category	Food Items	Inner zone			Middle zone			Outer zone			All zones					
		Cs	Ec	St	Cs	Ec	St	Cs	Ec	St	Cs	Ec	St			
Teleostei	Elopidae	—	—	—	0.01	—	—	—	—	—	—	—	—	<0.01	—	—
	Clupeidae	—	—	—	—	—	—	—	—	—	—	—	—	<0.01	—	—
	Engraulidae	0.91	—	—	0.01	—	—	0.03	—	—	—	—	—	<0.01	—	—
	Synodontidae	—	—	—	0.06	—	—	0.01	—	—	—	—	—	0.33	—	—
	Gerreidae	—	—	—	—	—	—	—	—	—	—	—	—	0.01	—	—
	Sciaenidae	—	—	—	—	—	—	0.01	—	—	—	—	—	<0.01	—	—
	<i>Cynoscion</i> sp.	0.01	—	—	0.24	—	—	—	—	—	—	—	—	<0.04	—	—
	<i>Micropogonias furnieri</i>	2.22	—	—	0.33	—	—	0.18	—	—	—	—	—	1.08	—	—
	Sciaenidae n.i.	1.10	—	—	—	—	—	—	—	—	—	—	—	0.19	—	—
	Gobiidae	6.25	—	—	5.33	—	—	0.75	—	—	—	—	—	4.46	—	—
Others	Paralichthyidae	—	—	—	—	—	—	0.02	—	—	—	—	—	<0.01	—	—
	Cynoglossidae	—	—	—	—	—	—	0.01	—	—	—	—	—	<0.01	—	—
	Teleostei n.i.	7.09	—	—	4.26	—	—	0.18	—	—	—	—	—	3.78	—	—
	Diatomacea	0.02	0.18	—	—	0.03	—	—	—	0.03	0.01	—	—	<0.01	0.05	0.01
	Eggs	—	—	—	—	—	—	—	—	<0.01	—	—	—	<0.01	—	—
	Plant	—	—	—	—	—	—	—	—	—	0.03	—	—	—	—	0.03
	Total number	72	41	8	62	121	3	39	139	54	173	301	65	—	—	—

n.i., not identified.

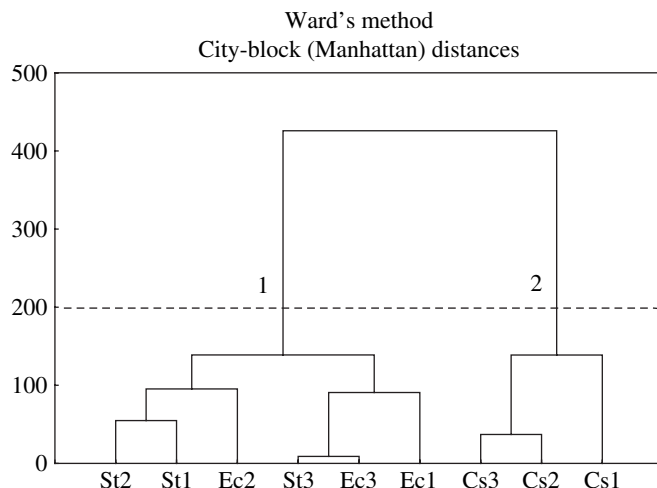


FIG. 4. Dendrogram resulting from the cluster analysis performed on stomach contents data (per cent index of relative importance) of three flatfish species (see Table III) grouped in zones (1, inner; 2, middle; 3, outer) of Sepetiba Bay.

Two feeding groups irrespective of  $L_S$  classes were shown by cluster analysis on the % $I_{RI}$  food items for the three species (Fig. 5). Group 1 was formed by *E. crossotus* and *S. tessellatus*, which showed significantly ( $P < 0.05$ ) higher values for Crustacea Isaeidae. Group 2 was composed of *C. spilopterus* only, which showed the highest % $I_{RI}$  values for Crustacea (Mysida, Brachyura and unidentified shrimps) and Teleostei when compared with other groups (Table IV).

TABLE IV. Significant  $F$ -values from ANOVA and Tukey's test for differences ( $P < 0.05$ ) of food items among the groups formed by cluster analysis for zones and standard length ( $L_S$ ) classes

Trophic category	Food Items	Zones			$L_S$ classes		
		$F$	$P$	$Pos-hoc$	$F$	$P$	$Pos-hoc$
Crustacea	Decapoda						
	Sergestidae	9.11	0.02	2 > 1	3.32	0.11	
	Shrimps n.i.	468.82	<0.01	2 > 1	101.63	<0.01	2 > 1
	Brachyura	0.39	0.55		10.08	0.02	2 > 1
	Mysida	24.89	<0.01	2 > 1	50.77	<0.01	2 > 1
Teleostei	Amphipoda						
	Isaeidae	15.43	0.01	1 > 2	39.24	<0.01	1 > 2
	Sciaenidae						
	<i>Micropogonias furnieri</i>	4.47	0.07		8.79	0.02	2 > 1
	Gobiidae	13.59	0.01	2 > 1	4.18	0.08	
Teleostei n.i.	8.55	0.02	2 > 1	15.99	0.01	2 > 1	

n.i., not identified.

## DIET OVERLAP

Generally, a small degree of dietary overlap was shown in all species. Diet overlaps between pairs of species were comparatively higher for *E. crossotus* and *S. tessellatus* (0.66) and for *C. spilopterus* and *E. crossotus* (0.58) (Table VI).

*Citharichthys spilopterus*, *E. crossotus* and *S. tessellatus* showed high dietary overlap in the inner zone between subadults and adults (0.84, 0.74 and 0.77, respectively). Furthermore, *E. crossotus* also showed higher dietary overlap between juveniles and subadults (0.92). In the middle zone, *C. spilopterus* showed higher dietary overlap between juveniles and subadults (0.98), while *E. crossotus* showed higher dietary overlap between juveniles and subadults (0.59) as well as between subadults and adults (0.75). In the outer zone, all three species showed high dietary overlap between all  $L_S$  classes (Table VII).

## DISCUSSION

The five most abundant species of flatfishes in Sepetiba Bay showed strong indications of partitioning of the available resources, sharing widespread feeding items, mainly Polychaeta Errantia. This item was used in large proportion by the two Achiridae species (*A. lineatus* and *T. paulistanus*), by *S. tessellatus* and *E. crossotus*, and to a lesser extent by *C. spilopterus*.

Polychaeta are a widely available resource in Sepetiba Bay. Their high occurrence in fish diets in the inner zone seems to avoid exploitation competition that would be likely to occur between closely related species of Achiridae. Some studies have reported the importance of Polychaeta in demersal and benthic fish food webs in sheltered and low turbulence areas (Kawakami & Amaral, 1983; Schafer *et al.*, 2002; Serrano *et al.*, 2003). The inner zone in Sepetiba Bay is the most sheltered area, where low turbulence enables high sedimentation of suspended matter, and where most of the substratum is muddy (Araújo *et al.*, 2002). Overall, Polychaeta are subsurface deposit-feeders belonging to a trophic group that typically attains high densities in environments in which turbulence is low and substantial amounts of organic material are able to settle and become incorporated into the subsurface sediment layer (Wildsmith *et al.*, 2005). Furthermore, the use of inner bay zone as feeding grounds by Achiridae suggests that this group can undergo harsh environmental conditions, taking advantage of the availability of resources. The advantage of living in shallow waters has been attributed to higher temperature, lower predation risks, abundant food and appropriate substrata (Minami & Tanaka, 1992).

Achiridae showed narrow trophic niche with specialization on Polychaeta Errantia. The use of Polychaeta by *A. lineatus* and *T. paulistanus* was also confirmed by Chaves & Serenato (1998) in Guaratuba Bay (Brazil) for the former species, and by Derrick & Kennedy (1997) in Chesapeake Bay (U.S.A.) for the congeneric *Trinectes maculatus* (Bloch & Schneider). Furthermore, crustaceans and other invertebrates have been reported in the diet of *A. lineatus* and *T. paulistanus* (Miller *et al.*, 1991).

Achiridae and Cynoglossidae are included in suborder Soleoidei that, according to the Regan–Norman model of Pleuronectiformes interrelationships (Hensley & Ahlstrom, 1984; Hensley, 1997), are reported to feed mainly on

TABLE V. Index of relative importance (%IRI) for food items of flatfish species (see Table III) by standard length ( $L_S$ ) classes in Setetiba Bay

Trophic category	Food Items	Juveniles ( $L_{S1}$ )			Subadults ( $L_{S2}$ )			Adults ( $L_{S3}$ )		
		Cs	Ec	St	Cs	Ec	St	Cs	Ec	St
Polychaeta	Polychaeta Sedentaria	—	1.09	—	—	4.11	0.04	—	3.86	—
	Polychaeta Errantia	—	12.12	—	3.40	22.69	42.27	8.52	32.76	18.93
	Tube of Polychaeta	—	—	—	—	—	0.06	—	—	0.94
Crustacea	Decapoda	—	—	—	—	—	—	0.22	—	—
	Penaidae	—	—	—	—	—	—	—	—	—
	Sergestidae	0.01	—	—	0.04	—	—	—	—	—
	Ogyrididae	—	—	—	<0.01	—	—	—	—	—
	Shrimps n.i.	14.62	0.82	—	9.68	0.41	—	16.33	0.09	—
	Brachyura larvae	—	0.10	—	0.10	0.05	—	0.01	<0.01	—
	Brachyura	0.34	0.04	—	3.71	0.01	—	5.53	0.05	0.08
	Anomura	—	<0.01	—	—	—	—	—	—	—
	Mysida	58.05	0.05	—	73.33	<0.01	—	33.03	—	—
	Cumacea	—	0.34	—	—	0.91	—	—	0.41	—
	Tanaidacea	—	—	—	—	—	—	—	<0.01	0.10
	Isopoda	0.09	11.81	—	<0.01	10.29	0.04	—	2.15	—
	Amphipoda	—	—	—	—	—	—	—	—	—
	Isaeidae	1.03	57.14	86.29	2.99	59.19	54.61	22.71	59.09	78.33
	Ampeliscidae	—	0.90	—	—	0.31	—	—	0.60	—
	Platyschnopsidae	—	—	—	—	—	—	—	—	0.07
Liljeborgiidae	—	<0.01	—	—	—	—	—	<0.01	—	
Caprellidae	0.17	1.07	13.71	0.12	0.79	2.91	0.02	0.91	0.96	
Copepoda	—	—	—	—	—	—	—	—	—	
Calanoida	21.09	14.48	—	0.01	1.11	0.02	<0.01	0.01	—	
Cyclopoida	—	<0.01	—	—	<0.01	—	—	<0.01	—	
Harpacticoida	—	0.01	—	—	<0.01	—	—	—	—	
Ostracoda	—	<0.01	—	<0.01	0.05	0.04	0.31	<0.01	0.49	
Crustacea fragments	—	—	—	—	—	—	—	—	0.03	

TABLE V. Continued

Trophic category	Food Items	Juveniles ( $L_{S1}$ )			Subadults ( $L_{S2}$ )			Adults ( $L_{S3}$ )		
		Cs	Ec	St	Cs	Ec	St	Cs	Ec	St
Teleostei	Elopidae	—	—	—	0.01	—	—	—	—	—
	Clupeidae	—	—	—	—	—	—	0.01	—	—
	Engraulidae	—	—	—	0.01	—	—	0.77	—	—
	Synodontidae	—	—	—	—	—	—	0.01	—	—
	Gerreidae	—	—	—	—	—	—	<0.01	—	—
	Sciaenidae	—	—	—	—	—	—	—	—	—
	<i>Cynoscion</i> sp.	0.64	—	—	0.03	—	—	0.01	—	—
	<i>Micropogonias furnieri</i>	2.64	—	—	<0.01	—	—	1.95	—	—
	Sciaenidae n.i.	0.03	—	—	0.43	—	—	0.06	—	—
	Gobiidae	0.20	—	—	1.39	—	—	7.54	—	—
	Paralichthyidae	0.11	—	—	—	—	—	—	—	—
	Cynoglossidae	0.05	—	—	—	—	—	—	—	—
	Teleostei n.i.	0.95	—	—	4.74	—	—	2.92	—	—
	Diatomacea	—	0.03	—	—	0.08	—	0.03	0.05	0.03
Others	Eggs	—	—	—	—	—	—	—	<0.01	—
	Plant	—	—	—	—	—	0.03	—	—	0.02
	Total number	35	112	2	65	106	28	74	83	35

n.i., not identified.

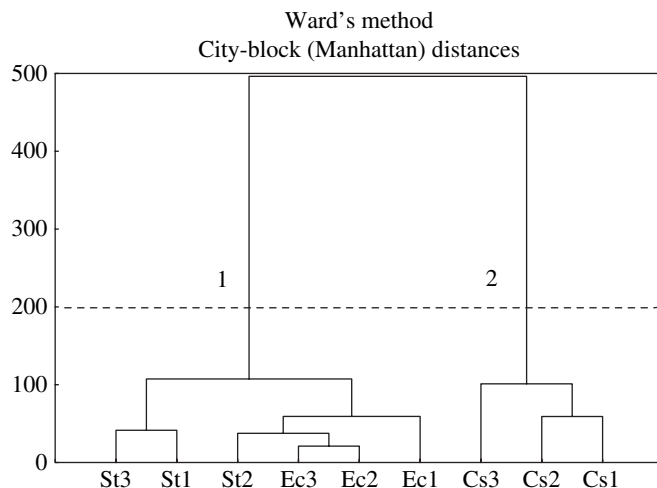


FIG. 5. Dendrogram resulting from the cluster analysis performed on stomach contents data (per cent index of relative importance) of three flatfish species (see Table III) of Sepetiba Bay grouped in standard length classes (1, juveniles; 2, subadults; 3, adults).

Polychaeta. Fishes that prey on Polychaeta usually have nocturnal habits and the ability to use the sense of smell and touch to catch the prey (Yazdani, 1969). *Citharichthys spilopterus* used Polychaeta Errantia in lower proportion than *S. tessellatus* in the inner zone; this is probably due to the ability to use other items like Mysida (19.85%  $I_{RI}$ ) and Calanoida (15.79%  $I_{RI}$ ) that have similar importance to Polychaeta Errantia (24.64%  $I_{RI}$ ). Additionally, *C. spilopterus* fed on another 13 items of minor importance in the inner zone, whereas *S. tessellatus* fed on another four items only, mainly Isaeidae amphipods (30.21%  $I_{RI}$ ).

*Etropus crossotus*, unlike the other four flatfish species, fed primarily on Isaeidae and secondarily on Polychaeta Sedentaria in the inner zone. On the other hand, Polychaeta Errantia is used by this species in large amounts in the middle and outer zones only. The limited occurrence of Achiridae in the middle and outer zones may favour the large use of this resource by *E. crossotus*, suggesting a generalized strategy. According to Reichert (2003), *E. crossotus* seemed to exploit this prey only marginally, despite the ample availability in a South Carolina (U.S.A.) estuary, possibly because this would require the fish

TABLE VI. Dietary overlap between five flatfish species represented by the simplified Morisita's index

Species	Al	Tp	Cs	Ec	St
<i>Achirus lineatus</i> (Al)	—	0.24	0.10	0.09	0.15
<i>Trinectes paulistanus</i> (Tp)	0.24	—	0.02	0.01	0.03
<i>Citharichthys spilopterus</i> (Cs)	0.10	0.02	—	0.58	0.19
<i>Etropus crossotus</i> (Ec)	0.09	0.01	0.58	—	0.66
<i>Symphurus tessellatus</i> (St)	0.15	0.03	0.19	0.66	—

TABLE VII. Simplified Morisita niche overlap between standard length ( $L_S$ ) classes ( $L_{S1}$ , juveniles;  $L_{S2}$ , subadults;  $L_{S3}$ , adults) of three flatfish species (see Table III) in Sepetiba Bay

Zones	$L_S$ classes	Species		
		Cs	Ec	St
Inner	$L_{S1} \times L_{S2}$	0.04	0.92	—
	$L_{S1} \times L_{S3}$	0.01	0.49	—
	$L_{S2} \times L_{S3}$	0.84	0.74	0.77
Middle	$L_{S1} \times L_{S2}$	0.98	0.59	—
	$L_{S1} \times L_{S3}$	0.43	0.15	—
	$L_{S2} \times L_{S3}$	0.49	0.75	0.46
Outer	$L_{S1} \times L_{S2}$	0.99	0.99	0.98
	$L_{S1} \times L_{S3}$	0.85	0.99	0.98
	$L_{S2} \times L_{S3}$	0.90	0.99	0.99

to move around in search of this sessile prey, probably increasing the risk of predation. Ambushing a continuous supply of zooplankton prey drifting by on the tidal current might be a strategy that is energetically more beneficial and may reduce predation risk.

The use of mobile items such as Mysida and shrimps by *C. spilopterus* is associated with the ability to use vision and to catch highly mobile prey with elaborate escape tactics, as reported by Yazdani (1969) and Braber & De Groot (1973) for species type 'turbot'. *Citharichthys spilopterus* was the only flatfish to use Teleostei as a food item. On the other hand, the large use of Amphipoda and Polychaeta Errantia by *E. crossotus* is associated with its ability to catch slow-moving, bottom-living prey (type 'plaice') and its smaller mouth-size, when compared with *C. spilopterus*.

*Symphurus tessellatus* used more diverse food items in the outer zone, where salinity was high. It broadly paralleled the findings of Allen & Baltz (1997) in Barataria Bay, Louisiana, U.S.A., which reported species of *Symphurus* having a strong affinity for high salinity areas. Amphipoda and Polychaeta were the main food items of *S. tessellatus*, which supports the findings of Wakabara *et al.* (2004). This is in full agreement with the results of Wakabara *et al.* (1982) for the congeneric *Symphurus jenysii* Evermann & Kendall of the south-east Brazilian coast. In spite of sharing some main food items with *E. crossotus*, it is unlikely that these two species compete directly for the same resources. Polychaeta and Amphipoda are probably abundant resources in Sepetiba Bay and these flatfishes have different secondary prey. It matches partially the findings of Nikolsky (1963), who reported that food competition in a faunistic assemblage is reduced by differential use of food items, and, in part, by spatial segregation in the area of distribution.

Although there is a considerable similarity in the gross taxonomic composition of the diets of Paralichthyidae and Cynoglossidae species, there are also marked differences in the proportions of the main taxonomic groups consumed by these species. High dietary overlapping between *E. crossotus* and *S. tessellatus* and between *C. spilopterus* and *E. crossotus* can be assumed to be biologically significant since their values are  $\geq 0.60$ . High dietary overlap must be interpreted

with caution as it does not necessarily mean competition for food resources between the two species compared (Sardiña & Cazorla, 2005). Assessment of whether or not dietary overlap between species is significant should take into consideration the abundance of the prey items of those species. Furthermore, dietary overlap tended to be highest for species pairings associated with the highest level of presumed niche similarity, which probably include *E. crossotus* and *S. tessellatus*. Conversely, unexpected low dietary overlap between members of the Achiridae was due to differential use of secondary items.

Intraspecific diet overlap was high for all three species (*C. spilopterus*, *E. crossotus* and *S. tessellatus*) in the outer zone only. The type of competition is determined largely by the distribution of the food resource in time and space (Milinski & Parker, 1991). If food items are distributed quite evenly, then competitive interactions are less likely than when they are clumped. As resource distributions become more heterogeneous, so do the distributions of those animals that require that resource, increasing the probability of the occurrence of direct interactions and competition. Resource partitioning in the outer zone is an indication of an even distribution of food availability in this part of Sepetiba Bay. Additionally, the proportional prey overlap among fishes may be even less if the prey are listed specifically rather than grouped into broad categories.

Fishes tend to catch larger and more energetic prey when they reach larger sizes, optimizing the energy budget, instead of pursuing smaller prey (Schoener, 1971). Paralichthyidae, *C. spilopterus* and *E. crossotus*, catch larger prey as they reach larger size. The relatively low competition for resources among fishes with a large mouth gape allows them to coexist without any segregation along the spatial dimension (Piet *et al.*, 1998) and this seems to be the case for these two species, whose main food item was the same in all  $L_S$  classes, but larger individuals incorporated secondary items in diet. Small-sized *C. spilopterus* used secondarily Calanoida (21.09%  $I_{RI}$ ) and the largest ones, Isaeidae amphipods (22.71%  $I_{RI}$ ) and large amounts of fishes. Such changes in diet closely match the optimal forage theory, since each gram of fish contains more proteins, lipids and energy than 1 g of crustaceans (Jobling, 1995). These findings are in accordance with Reichert & Van der Veer (1991) along the east coast of Georgia (U.S.A.) and with Castillo-Rivera *et al.* (2000) in the Western Gulf of México, who reported increasing larger prey for larger fishes. Likewise, small *E. crossotus* fed secondarily on Calanoida (14.48%  $I_{RI}$ ), whereas the largest ones fed on Polychaeta Errantia (32.76%  $I_{RI}$ ), which is in accordance with Wakabara *et al.* (1982) for the diet of the congeneric *Etopus longimanus* Norman. Increasing flatfish size is probably the main factor associated with both dietary changes that include the ability to eat larger macrobenthic prey (Andersen *et al.*, 2005).

In spite of using the most diverse items (26), *C. spilopterus* did not show the broadest niche width among the species studied, and it is associated with a lower evenness in the consumption of the items, when compared with *E. crossotus* that showed the broadest niche width despite using only 20 items. The Shannon–Wiener index suffers, however, from combining two distinct facets of diversity–species richness and the way individuals are distributed among species (evenness). These two facets may work in opposite directions, and their effects are confounding.



Differences in the Pleuronectiformes' diet composition along with spatial and size changes in the use of the available resources contributed to allow their coexistence in Sepetiba Bay. The use of a high diversity of food by flatfishes is an indication of the absence of interspecific competitive interactions. Furthermore, recent studies on the feeding ecology of flatfishes suggested that interspecific competition for food was unlikely (Beyst *et al.*, 1999; Amara *et al.*, 2001) and it matches with the findings of this work.

Habitat quality and quantity clearly have the potential to affect the richness and abundance of flatfish populations (Gibson, 1994). The increasing anthropogenic pressure in Sepetiba Bay may jeopardize the habitat quality in the near future. Dredging of the access channel to enhance Sepetiba Port capacity increases the transport of sediment and it is a major pressure on the demersal fishes. Furthermore, discharge into Sepetiba Bay has been modified by a large-scale water diversion scheme, which has impacted several smaller drainage basins (Molisani *et al.*, 2006). Therefore, further studies on the use of Sepetiba Bay by flatfish populations could be performed to detect anthropogenic influences on resource partitioning. Another nine flatfish species of the bay have been reported (Mendonça & Araújo, 2002), although no information on their diet is available, probably due to their relatively low abundance in the area. As a concluding remark, it could be pointed out that the five flatfish species in Sepetiba Bay have different diets, and in spite of the fact that certain prey types are consumed by more than one species, no evidence of food competition was found between them.

We thank biologist M. C. C. Azevedo, A. L. M. Pessanha and P. Mendonça for helping in fieldwork. This paper is a portion of the first authors's M.Sc. Dissertation submitted to the Animal Biology Programme of the University Federal Rural of Rio de Janeiro. This work was partially supported by CNPq – Brazilian National Agency for Scientific and Technological Development (Proc. 474813-03-7).

## References

- Aarnio, K., Bonsdorff, E. & Rosenback, N. (1996). Food and feeding habits of juvenile flounder *Platichthys flesus* (L.), and turbot *Scophthalmus maximus* L. in the Aland Archipelago, northern Baltic Sea. *Journal of Sea Research* **36**, 311–320. doi: 10.1016/S1385-1101(96)90798-4
- Allen, R. L. & Baltz, D. M. (1997). Distribution and microhabitat use by flatfishes in a Louisiana estuary. *Environmental Biology of Fishes* **50**, 85–103. doi: 10.1023/A:1007398517163
- Amara, R., Laffargue, P., Dewarumez, J. M., Maryniak, C., Lagardère, F. & Luczac, C. (2001). Feeding ecology and growth of 0-group flatfish (sole, dab and plaice) on a nursery ground (Southern Bight of the North Sea). *Journal of Fish Biology* **58**, 788–803. doi: 10.1006/jfbi.2000.1498
- Amezua, F., Nash, R. D. M. & Veale, L. (2003). Feeding habits of the Order Pleuronectiformes and its relation to the sediment type in the north Irish Sea. *Journal of the Marine Biological Association of the United Kingdom* **83**, 593–601. doi: 10.1017/S0025315403007525h
- Amundsen, P. A., Gabler, H. M. & Staldvik, F. J. (1996). A new approach to graphical analysis of feeding strategy from stomach contents data – modification of the Costello (1990) method. *Journal of Fish Biology* **48**, 607–614. doi: 10.1111/j.1095-8649.1996.tb01455.x

- Andersen, B. S., Carl, J. D., Gronkjaer, P. & Stottrup, J. G. (2005). Feeding ecology and growth of age 0 year *Platichthys flesus* (L.) in a vegetated and bare sand habitat in a nutrient rich fjord. *Journal of Fish Biology* **66**, 531–552. doi: 10.1111/j.1095-8649.2005.00620.x
- Araújo, F. G., Azevedo, M. C. C., Silva, M. A., Pessanha, A. L. M., Gomes, I. D. & Cruz-Filho, A. G. (2002). Environmental influences on the demersal fish assemblages in the Sepetiba Bay, Brazil. *Estuaries* **25**, 441–450.
- Azevedo, M. C. C., Araújo, F. G., Pessanha, A. L. M. & Silva, M. A. (2006). Co-occurrence of demersal fishes in a tropical bay in southeastern Brazil: a null model analysis. *Estuarine Coastal and Shelf Science* **66**, 315–322. doi: 10.1016/j.eess.2005.09.006
- Baltz, D. M. & Jones, R. F. (2003). Temporal and spatial patterns of microhabitat use by fishes and decapod crustaceans in a Louisiana estuary. *Transactions of the American Fisheries Society* **132**, 662–678. doi: 10.1577/T00-175
- Berg, J. (1979). Discussion of methods of investigating the food of fishes, with reference to a preliminary study of the prey of *Gobiusculus flavescens* (GOBIIDAE). *Marine Biology* **50**, 263–273. doi: 10.1007/BF00394208
- Beyst, B., Cattrusse, A. & Mees, J. (1999). Feeding ecology of juvenile flatfishes of the surf zone of a sandy beach. *Journal of Fish Biology* **55**, 1171–1186. doi: 10.1111/j.1095-8649.1999.tb02068.x
- Braber, L. & De Groot, S. J. (1973). On the morphology of the alimentary tract of flatfishes (Pleuronectiformes). *Journal of Fish Biology* **5**, 147–153. doi: 10.1111/j.1095-8649.1973.tb04443.x
- Castillo-Rivera, M., Kobelkowsky, A. & Chávez, A. M. (2000). Feeding biology of the flatfish *Citharichthys spilopterus* (Bothidae) in a tropical estuary of Mexico. *Journal of Applied Ichthyology* **16**, 73–78. doi: 10.1046/j.1439-0426.2000.00151.x
- Chaves, P. T. C. & Serenato, A. (1998). Diversity in diet of flatfishes assemblages (Teleostei, Pleuronectiformes) in a mangrove area in the Guaratuba Bay, Paraná, Brasil. *Revista Brasileira de Oceanografia* **46**, 61–68 (in Portuguese).
- Clark, M. R. (1985). The food and feeding of seven fish species from Campbell Plateau, New Zealand. *Journal of Marine and Freshwater Research* **19**, 339–363.
- Cortès, E. (1997). A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. *Canadian Journal of Fisheries and Aquatic Sciences* **54**, 726–738.
- Derrick, P. A. & Kennedy, V. S. (1997). Prey selection by the hogchoker, *Trinectes maculatus* (Pisces: Soleidae), along summer salinity gradients in Chesapeake Bay, USA. *Marine Biology* **129**, 699–712. doi: 10.1007/s002270050213
- Figueiredo, J. L. & Menezes, N. A. (2000). *Catalogue of Marine Fishes from Southeastern Brazil. IV. Teleostei (5)*. São Paulo: Museum of Zoology, Universidade de São Paulo (in Portuguese).
- Garrison, L. P. & Link, J. S. (2000). Dietary guild structure of the fish community in the Northeast United States continental shelf ecosystem. *Marine Ecology Progress Series* **202**, 231–240. doi: 10.3354/meps202231
- Gibson, R. N. (1994). Impact of habitat quality and quantity on the recruitment of juvenile flatfishes. *Netherlands Journal of Sea Research* **32**, 191–206. doi: 10.1016/0077-7579(94)90040-X
- Gibson, R. N. (2005). *Flatfishes: Biology and Exploitation*. Oxford: Blackwell Publishing.
- Gibson, R. N. & Robb, L. (1992). The relationship between body size, sediment grain size and the burying ability of juvenile plaice, *Pleuronectes platessa* L. *Journal of Fish Biology* **40**, 771–778. doi: 10.1111/j.1095-8649.1992.tb02623.x
- Guedes, A. P. P., Araújo, F. G. & Azevedo, M. C. C. (2004). Estratégia trófica dos linguados *Citharichthys spilopterus* Günther e *Symphurus tessellatus* (Quoy & Gaimard) (Actinopterygii, Pleuronectiformes) na Baía de Sepetiba, Rio de Janeiro, Brasil. *Revista Brasileira de Zoologia* **21**, 857–864 (in Portuguese).
- Hensley, D. A. (1997). An overview of the systematics and biogeography of the flatfishes. *Journal of Sea Research* **37**, 187–194. doi: 10.1016/S1385-1101(97)00017-8

- Hensley, D. A. & Ahlstrom, E. H. (1984). Pleuronectiformes: relationships. In *Ontogeny and Systematics of Fishes* (Moser, H. G., Richards, W. J., Cohen, D. M., Fahay, M. P., Kendall, A. W. Jr & Richardson, S. L., eds), pp. 670–687. Lawrence, TX: American Society of Ichthyology and Herpetology.
- Hyslop, E. J. (1980). Stomach contents analysis: a review of methods and their applications. *Journal of Fish Biology* **17**, 411–429. doi: 10.1111/j.1095-8649.1980.tb02775.x
- Jobling, M. (1995). *Environmental Biology of Fishes*. London: Chapman & Hall.
- Kawakami, E. & Amaral, A. C. Z. (1983). Importance of annelids Polychaeta in feeding habits of *Etropus longimanus* Norman, 1908 (Pisces, Pleuronectiformes). *Iheringia (Serie Zoologia)* **62**, 47–54 (in Portuguese).
- Krebs, C. J. (1989). *Ecological Methodology*. New York: Harper and Row.
- Labropoulou, M. & Eleftheriou, A. (1997). The foraging ecology of two pairs of congeneric demersal fish: importance of morphological characteristics in prey selection. *Journal of Fish Biology* **50**, 324–340. doi: 10.1111/j.1095-8649.1997.tb01361.x
- Leal Neto, A. C., Legey, L. F. L., González-Araya, M. C. & Jablonski, S. (2006). A system dynamics model for the environmental management of the Sepetiba Bay watershed, Brazil. *Environmental Management* **38**, 879–888. doi: 10.1007/s00267-005-0211-5
- Mendonça, P. & Araújo, F. G. (2002). Composição das populações de linguados (Osteichthyes, Pleuronectiformes) da Baía de Sepetiba, Rio de Janeiro, Brasil. *Revista Brasileira de Zoologia* **19**, 339–347 (in Portuguese).
- Milinski, M. & Parker, G. A. (1991). Competition for resources. In *Behavioural Ecology: an Evolutionary Approach* (Krebs, J. R. & Davies, N. B., eds), pp. 137–168. London: Blackwell Scientific.
- Miller, J. M., Burke, J. S. & Fitzhugh, G. R. (1991). Early life history patterns of Atlantic North American flatfish: likely (and unlikely) factors controlling recruitment. *Netherlands Journal of Sea Research* **27**, 261–275. doi: 10.1016/0077-7579(91)90029-Z
- Minami, T. & Tanaka, M. (1992). Life history cycles in flatfish from the northwestern Pacific, with particular reference to their early life histories. *Netherlands Journal of Sea Research* **29**, 35–48. doi: 10.1016/0077-7579(92)90006-Z
- Molisani, M. M., Kjerfve, B., Silva, A. P. & Lacerda, L. D. (2006). Water discharge and sediment load to Sepetiba Bay from an anthropogenically-altered drainage basin, SE Brazil. *Journal of Hydrology* **331**, 425–433. doi: 10.1016/j.jhydrol.2006.05.038
- Munroe, T. A. (1998). Systematics and ecology of tonguefishes of the genus *Symphurus* (Cynoglossidae: Pleuronectiformes) from the western Atlantic Ocean. *Fishery Bulletin* **96**, 1–182.
- Nikolsky, G. V. (1963). *The Ecology of Fishes*. London: Academic Press.
- Piet, G. J., Pfisterer, A. B. & Rijnsdorp, A. D. (1998). On factors structuring the flatfish assemblage in the southern North Sea. *Journal of Sea Research* **40**, 143–152. doi: 10.1016/S1385-1101(98)00008-2
- Pinkas, L., Oliphont, M. S. & Iverson, I. L. K. (1971). Food habits of albacore, bluefin tuna and bonito in California waters. *California Fish Game* **152**, 1–105.
- Reichert, M. J. M. (1998). *Etropus crossotus*, an annual flatfish species; age and growth of the fringed flounder in South Carolina. *Journal of Sea Research* **40**, 323–332. doi: 10.1016/S1385-1101(98)00022-7
- Reichert, M. J. M. (2003). Diet, consumption and growth of juvenile fringed flounder (*Etropus crossotus*): a test of the ‘maximum growth/optimum food hypothesis’ in a subtropical nursery area. *Journal of Sea Research* **50**, 97–116. doi: 10.1016/S1385-1101(03)00081-9
- Reichert, M. J. M. & Van der Veer, H. W. (1991). Settlement, abundance, growth and mortality of juvenile flatfish in a subtropical tidal estuary (Georgia, U.S.A.). *Netherlands Journal of Sea Research* **27**, 375–391. doi: 10.1016/0077-7579(91)90040-8
- Ross, S. T. (1986). Resource partitioning in fish assemblages: a review of field studies. *Copeia* **1986**, 352–388.

- Sardiña, P. & Cazorla, A. L. (2005). Feeding interrelationships and comparative morphology of two young sciaenids co-occurring in South-western Atlantic waters. *Hydrobiologia* **548**, 41–49. doi: 10.1007/s10750-005-3643-2
- Schafer, L. N., Platell, M. E., Valesini, F. J. & Potter, I. C. (2002). Comparisons between the influence of habitat type, season and body size on the dietary compositions of fish species in nearshore marine waters. *Journal of Experimental Marine Biology and Ecology* **278**, 67–92. doi: 10.1016/S0022-0981(02)00337-4
- Schoener, T. W. (1971). Theory of feeding strategies. *Annual Review of Ecology and Systematics* **2**, 369–404.
- Schoener, T. W. (1974). Resource partitioning in natural communities. *Science* **185**, 27–39. doi: 10.1126/science.185.4145.27
- Serrano, A., Velasco, F. & Olaso, I. (2003). Polychaete annelids in the diet of demersal fish from the southern shelf of the Bay of Biscay. *Journal of the Marine Biological Association of the United Kingdom* **83**, 619–623. doi: 10.1017/S0025315403007550h
- Toepfer, C. S. & Fleeger, J. W. (1995). Diet of juvenile fishes *Citharichthys spilopterus*, *Symphurus plagiatus* and *Gobionellus boleosoma*. *Bulletin of Marine Science* **56**, 238–249.
- Vicentini, R. N. & Araújo, F. G. (2003). Sex ratio and size structure of *Micropogonias furnieri* (Desmarest, 1823) (Perciformes, Sciaenidae) in Sepetiba Bay, Rio de Janeiro, Brazil. *Brazilian Journal of Biology* **63**, 559–566.
- Wakabara, Y., Kawakami de Resende, E. & Tararam, A. S. (1982). Amphipods as one of the main food components of three Pleuronectiformes from the continental shelf of south Brazil and north Uruguay. *Marine Biology* **68**, 67–70. doi: 10.1007/BF00393142
- Wildsmith, M. D., Potter, I. C., Valesini, F. J. & Platell, M. E. (2005). Do the assemblages of benthic macroinvertebrates in nearshore waters of Western Australia vary among habitat types, zones and seasons? *Journal of the Marine Biological Association of the United Kingdom* **85**, 217–232. doi: 10.1017/S0025315405011100h
- Yazdani, G. M. (1969). Adaptation in the jaws of flatfish (Pleuronectiformes). *Journal of Zoology* **159**, 181–222.
- Zar, J. H. (1999). *Biostatistical Analysis*. Englewood Cliffs, NJ: Prentice-Hall.