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Partitioning of the feeding niche along spatial, seasonal and size dimensions by the fish community in a tropical Bay in Southeastern Brazil

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Abstract

Feeding guilds and spatial, seasonal and ontogenetic changes in the diets of 24 fish species in a tropical bay in Southeastern Brazil were examined. The hypotheses tested were that groups of species form specific trophic guilds and that the feeding partitioning differs along the niche dimensions. Five trophic guilds (Polychaeta, Copepoda, Teleostei, Teleostei/Crustacea and Polychaeta/Crustacea) and two species with specialised feeding, one teleost (*Aspistor lunicutis*) and one bivalvia (*Spherooides testudineus*), were found. Polychaeta was the most important resource for nine fish species, followed by Copepoda (6 spp.), Teleostei (5 spp.) and Caprellidae Amphipoda (3 spp.). Polychaeta was the most used resource for species in the inner bay zone, and Crustaceans in the outer bay zone. We detected a predominance of Polychaeta between the spring and autumn, whereas crustaceans were consumed at a greater rate in the winter. The most conspicuous changes in diet occurred along the spatial and seasonal dimensions, rather than the size dimensions. The hypotheses tested were accepted. Identifying and incorporating information about the bay food web is a first step towards developing management strategies that are sensitive to this particular ecosystem.

Introduction

Knowledge of the trophic ecology of fish species in coastal systems is fundamental to understanding the functional roles of different components of fish assemblages (Blaber 1997; Cruz-Escalona *et al.* 2000). The feeding relationships between fish species are critical for understanding the dynamics of community structure as well as for developing management approaches for the conservation and sustainable use of biological diversity (Micheli & Halpern 2005; Greenstreet & Rogers 2006).

A group of species that exploits the same class of environmental resources in a similar way has been defined as a guild (Root 1967). Members of a guild interact strongly with each other but only weakly with members of other guilds (Pianka 1980; Jaksic & Medel 1990). Food has been

shown to be the most important resource partitioned among species (Ross 1986), and the trophic organisation of fish assemblages has been widely discussed as a possible strategy either to avoid competition (Pianka 1980; Angel & Ojeda 2001) or to optimise the use of the available resources (Jaksic 1981).

Spatial factors greatly affect the trophic organisation of the fish community in a particular area (Elliott *et al.* 2002). As feeding resources are distributed in patches along the spatial dimensions (MacArthur & Pianka 1966; Schoener 1971; Meyer & Posey 2009), it is reasonable to suppose that the spatial distribution of the fish community follows resource availability and that this niche dimension is a major determinant of community spatial distribution. Fish may have to choose between a habitat that provides more abundant and diverse prey, but in

which prey are harder to capture, and a habitat with lower prey abundance but better capture opportunities (Crowder & Cooper 1982).

Seasonal changes in the diets of fishes are frequently attributed to changes in either the life-cycle patterns of the prey or the feeding activity of the predators (Snyder 1984; Lucena *et al.* 2000), whereas ontogenetic changes reflect adaptations that use the available resources and minimise intraspecific competition (Schoener 1974). The seasonal coincidence of peak fish abundance and secondary production suggests that food availability may be a principal factor influencing the nursery function of shallow inshore habitats (Barry *et al.* 1996). Ontogenetic changes in diet have been reported for many different species (McAfee & Morgan 1996; Muñoz & Ojeda 1998; Hajisamae 2009) because fish exhibit indeterminate growth that results in body sizes spanning orders of magnitude within one species, and size is directly related to risk of predation and foraging ability (Werner 1984; Ross 1986).

Many food web comparisons have been based on snapshots of the community that have failed to reveal variation over time and space (Akin & Winemiller 2006). Detailed trophic ecology studies that explore the three niche dimensions (spatial, seasonal and size) are necessary to provide information for management policies concerning these renewable resources. The aim of this study was to describe the diet and trophic organisation of the

bottom fish community in a tropical bay in Southeastern Brazil, in terms of guilds and spatial, seasonal and ontogenetic changes. We tested two hypotheses: (i) that the abundant species partition available resources along spatial, temporal and size dimensions and (ii) that groups of species form specific trophic guilds both to optimise the use of resources and to allow species to coexist. We selected 24 abundant species caught in experimental bottom trawls, and posed the following questions: (i) Are the species organised in trophic guilds? (ii) Are there changes in feeding partitioning along the spatial, seasonal and ontogenetic dimensions? (iii) If so, what are the most conspicuous changes in those niche dimensions?

Material and Methods

Study area

Sepetiba Bay ($22^{\circ}549'–23^{\circ}049' S$; $43^{\circ}349'–44^{\circ}109' W$) is located in Rio de Janeiro State, Southeastern Brazil (Fig. 1), and has an area of 520 km^2 , which encompasses a wide range of habitats, including mangroves, sandbanks and small estuarine areas (Fizman *et al.* 1984; Leal Neto *et al.* 2006). The overall depth is $<5 \text{ m}$, the waters are rich in organic nutrients from continental drainage, and the bottom is predominantly muddy. This microtidal system has tides ranging from 0.5 to 1.5 m. The bay supports a rich and diversified fish fauna and is used as a

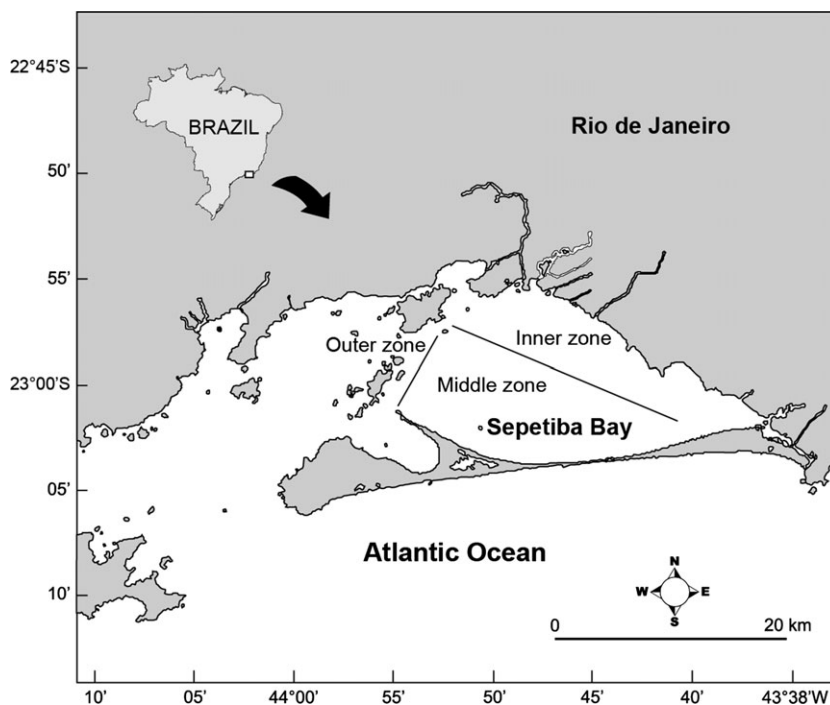


Fig. 1. Study area, Sepetiba Bay indicating the three sampling zones (inner, middle and outer).

rearing ground for several coastal fish species. A total of 148 fish species have been recorded in the bay (Araújo *et al.* 2002) but little information on their trophic ecology is available (e.g. Santos & Araújo 1997; Guedes *et al.* 2004; Guedes & Araújo 2008). In the last decade, the bay has suffered increased degradation due to industrial outflow and municipal effluents brought into the bay by rivers and drainage channels on the outskirts of the city of Rio de Janeiro.

The bay can be divided into three zones (inner, middle and outer), according to depth, salinity gradient and human influence (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 that are usually <5 m, and an average salinity of 28. The outer zone, located near the sea, exhibits contrasting environmental conditions: a mainly sandy substratum, comparatively lower temperatures and higher salinity and transparency; the maximum depth is c. 28 m, and the average salinity is 33. The middle zone displays intermediate environmental conditions between the inner and the outer zones.

Sampling and data handling

Fish were sampled quarterly by bottom trawling in July (winter) and October (spring) of 2000, and February (summer) and May (autumn) of 2001. Three replicate fish samples were taken in each zone and season. Tows were against the current, with a duration of 20 min at the bottom and a towing speed of c. 3 km·h⁻¹, which covered a distance of approximately 1500 m. The trawl had an 8 m headline, 11 m ground rope, 25 mm stretched mesh and 12 mm mesh cod-end liner. The bottom depth in the areas trawled ranged from 4 to 25 m.

Immediately after collection, fishes were anaesthetised in benzocaine hydrochloride (50 mg·l⁻¹) and fixed in 10% formaldehyde–seawater solution. After 48 h, they were transferred to 70% ethanol. All fish were identified to the lowest possible taxonomic level, measured for standard length (mm) and weighed (g). The most abundant species (24 species), *i.e.* those that accounted for >1% of the total number of fishes and >20% of frequency of occurrence, were chosen for this study because they are more likely to occur in different size ranges in all bay zones and seasons. The stomachs were removed from the fish, and food items were identified under a stereomicroscope. Each identified food item was separated, counted and weighted at a precision of 0.001 g. For each of the four items weighing <0.001 g, the weight was assumed to be 0.001 g. Identification of invertebrates follows Ruppert & Barnes (1996) and Brusca & Brusca (2003).

Data analysis

The stomach contents of 24 species were analysed from individuals covering the three bay zones, four seasons and three size classes (SL, standard length in mm). These size classes correspond to the juvenile period (SL₁), the maturing period (SL₂) and the adult period (SL₃) of each fish species (see Table 1). If a sample consisted of <15 individuals of each species, all stomachs were dissected and examined. In samples with >15 fish of a species, 15 individuals, including the smallest and the largest, covering a wide size range from each zone in each season were selected for dissection. In some exceptional cases, spatial, seasonal or size comparisons were not performed owing to the low number of individuals. Fish with empty stomachs or those with unidentifiable contents were excluded from the analyses.

The index of relative importance (IRI), proposed by Pinkas *et al.* (1971), uses the frequency of occurrence, percent of total number and percent of weight or volume (Berg 1979; Hyslop 1980; Clark 1985). This procedure conveys various types of information on the feeding habits and describes the relative contribution of stomach contents in the diet. The IRI was calculated as: $IRI = (\%N + \%P) \times \%FO$ and was expressed on a percent basis, such that %IRI for a given food item, *i* (IRI_{*i*}), becomes

$$\%IRI_i = 100 \times IRI_i / \sum_{i=1}^n IRI_i$$

where *n* is the total number of food items considered at a given taxonomic level (Cortés 1997). Food items with %IRI <1% and digested material were excluded from the analyses. The dominant items, *i.e.* those with IRI >20%, were used to interpret spatial, seasonal and ontogenetic changes.

Resource partitioning

One-way analysis of variance (ANOVA) was used to compare dietary items that had %IRI >1% among the three niche dimensions (spatial, seasonal and size). When significant differences (*P* < 0.05) were detected by ANOVA, a Tukey's test was used to determine differences in mean values following ANOVA. In addition, a non-parametric multivariate permutational analysis of variance (PERMANOVA) on the Bray–Curtis similarity matrix was used to investigate differences in the diet and to assess eventual interactions between factors at a significance level of $\alpha = 0.05$. Some species were not included in this analysis because individuals of these species did not exist at different levels.

Table 1. List of species, number of individuals (n), standard length (SL, mm) range and size classes (in mm) used in diet analysis.

Scientific name	Code	n	Size classes			SL range	Source
			SL ₁	SL ₂	SL ₃		
<i>Achirus lineatus</i> (Linnaeus, 1758)	Al	20	<95	95–110	>110	75–119	This study
<i>Aspistor luniscutis</i> (Valenciennes, 1840)	Au	181	<180	180–220	>220	95–315	Gomes (2000)
<i>Cathorops spixii</i> (Spix and Agassiz, 1829)	Cp	96	<140	140–185	>185	77–259	Corrêa (2001)
<i>Chloroscombrus chrysurus</i> (Linnaeus, 1766)	Cc	88	<130	130–160	>160	81–185	Panfili <i>et al.</i> (2006)
<i>Citharichthys spilopterus</i> Günther, 1862	Cs	20	<110	110–125	>125	98–162	Dias <i>et al.</i> (2005)
<i>Ctenosciaena gracilicirrus</i> (Metzelaar, 1919)	Cg	260	<75	75–100	>100	51–139	This study
<i>Cynoscion leiarchus</i> (Cuvier, 1830)	Cl	78	<100	100–180	>180	57–218	Shlossman & Chittenden (1981)
<i>Dactylopterus volitans</i> (Linnaeus, 1758)	Dv	85	<115	>115	–	77–156	This study
<i>Diapterus rhombeus</i> (Cuvier, 1829)	Db	207	<95	95–135	>135	56–235	Etchevers (1978)
<i>Diplectrum radiale</i> (Quoy and Gaimard, 1824)	Dr	29	<110	110–135	>135	61–210	Bubley (2004)
<i>Etropus crossotus</i> Jordan and Gilbert, 1882	Ec	64	<85	85–105	>105	67–150	Sánchez-Gil <i>et al.</i> (2008)
<i>Eucinostomus argenteus</i> Baird and Girard, 1855	Ea	161	<95	95–120	>120	55–158	Poot-Salazar <i>et al.</i> (2009)
<i>Eucinostomus gula</i> (Quoy and Gaimard, 1824)	Eg	113	<95	95–130	>130	68–178	Poot-Salazar <i>et al.</i> (2009)
<i>Genidens genidens</i> (Cuvier, 1829)	Gg	60	<140	140–180	>180	106–194	Gomes (2000)
<i>Harengula clupeola</i> (Cuvier, 1829)	Hc	67	<100	100–135	>135	71–188	García-Abad <i>et al.</i> (1999)
<i>Menticirrus americanus</i> (Linnaeus, 1758)	Ma	147	<85	85–120	>120	53–260	Santos (2006)
<i>Micropogonias furnieri</i> (Desmarest, 1823)	Mf	259	<170	170–205	>205	41–258	Castello (1986)
<i>Prionotus punctatus</i> (Bloch, 1793)	Pp	145	<100	>100	–	30–145	Froese & Pauly (2009)
<i>Selene setapinnis</i> (Mitchill, 1815)	Ss	66	<120	120–140	>140	43–193	McEachran & Fechhelm (2005)
<i>Spherooides testudineus</i> (Linnaeus, 1758)	Sd	77	<100	100–160	>160	35–244	Rocha <i>et al.</i> (2002)
<i>Stellifer rastrifer</i> (Jordan, 1889)	Sr	159	<90	90–115	>115	55–183	Santos (2006)
<i>Symphurus tessellatus</i> (Quoy and Gaimard, 1824)	St	80	<115	115–140	>140	100–205	Munroe (1998)
<i>Trichiurus lepturus</i> Linnaeus, 1758	Tl	40	<400	>400	–	166–620	Martins & Haimovici (1997)
<i>Trinectes paulistanus</i> (Miranda Ribeiro, 1915)	Tp	10	–	<110	>110	96–136	He & Stewart (2001)
Total		2512					

Size classes: SL₁ = juveniles; SL₂ = subadults; SL₃ = adults. References for size classes are also indicated.

Cluster analysis was used as a classification method to group individuals from samples where similar patterns in diet could be observed and, consequently, the existence of trophic segregation among the species was demonstrated. Values of %IRI were square-root transformed, and the Bray–Curtis similarity matrix was constructed. The resulting similarity matrix was used to construct a dendrogram using the group-average method, and a permutation similarity test (SIMPROF) was used to test each node of the dendrogram for statistical significance.

Species clustered in a given group were compared by similarity analyses (ANOSIM) to detect any significant differences among the groups. ANOSIM is based on ranking similarity among the samples in the similarity matrix and tests the null hypothesis that the mean ranking of similarity within the groups is not different from the mean ranking similarity among the groups. Groups that were significantly different ($P < 0.05$) were analysed by the similarity percentage routine (SIMPER) to identify items that were typical of the group. The SIMPER routine calculated the average similarity within each group and determined the percentage contribution of each item to the overall group similarity (Laidig *et al.* 2009). We considered fish to be part of consistent feeding groups within

each dimension (spatial, seasonal and size) if they had average similarities of >70%. To assess the relative importance of changes in the three feeding dimensions, matrices of diet (as %IRI) and species similarity were compared between zones, seasons and sizes with Mantel-type permutation tests (999 permutations) using the RELATE routine. Correlations (ρ) between matrices in the RELATE routine were calculated using the Kendall rank correlation method. These analyses were performed using the statistical package PRIMER version 6.0 (Clarke & Gorley 2006).

Results

Four species (*Diapterus rhombeus*, *Eucinostomus argenteus*, *Eucinostomus gula* and *Menticirrus americanus*) fed mainly on Polychaeta in the inner zone compared with the middle and outer zones, whereas six species (*D. rhombeus*, *E. argenteus*, *M. americanus*, *Selene setapinnis* and *Spherooides testudineus*) fed more on Crustaceans (Amphipoda, Caprellidae, Copepoda and Decapoda) in the outer zone than in the inner zone, according to ANOVA (Table 2). Crustaceans were consumed at a greater rate by seven species (*Aspistor luniscutis*, *Ctenosciaena*

Table 2. Results of one-way ANOVA comparing diets of 24 fish species from zones, seasons and sizes. Analyses were performed on %IRI values.

Species	Item	Zones		Seasons		Sizes	
		F	Post-hoc	F	Post-hoc	F	Post-hoc
Au	Brachyura	4.2*	O > I, M				
	Copepoda			3.7*	W > S		
	Polychaeta	4.3*	O > M				
Cc	Copepoda	798.0***	M > O > I				
Cg	Amphipoda			4.4*	W > P		
	Isopoda			4.5*	S > P, W		
Cp	Algae	7.2**	O > I, M				
	Bivalvia	6.7**	O > I, M				
	Copepoda			5.1*	P > S, A		
	Polychaeta			5.4**	A > W, P, S		
Db	Teleost crystalline	5.9*	O > I, M				
	Caprella	8.2**	O > I, M				
	Copepoda	5.6*	M > I				
	Ostracoda			3.9*	S > A		
	Plant			3.4*	S > A		
Dv	Polychaeta	6.1*	I > M, O				
	Amphipoda			4.0*	W > P		
	Cumacea			24.0***	A > W, P, S		
	Decapoda			25.0***	S > W, P, A		
Ea	Isopoda			1440.0***	S > W, P, A		
	Caprella	7.1**	O > I				
	Copepoda					3.9*	J > A
	Polychaeta	4.7*	I > M, O				
Ec	Caprella	6.7**	M > I				
	Cumacea	6.9**	M > I, O				
	Isopoda			4.6*	S > P, A		
Eg	Copepoda	4.3*	M > I				
	Polychaeta	5.5*	I > M				
Gg	Caprella	216.4***	M > I				
	Ostracoda	6.1*	I > M				
	Plant			8.8*	P > W		
Hc	Caprella			961.0***	P > W, S, A		
	Copepoda			5.7*	A > W		
	Crustacea larvae			4.5*	P > A		
	Diatomacea			3.8*	S > A		
	Teleostei			37.6***	W > P, u, A		
	Teleost egg			3.7*	W > A		
Ma	Amphipoda	8.0**	O > I	3.6*	W > P, A		
	Polychaeta	10.7***	I > M, O				
	Tanaidacea			4.3*	P > W, A		
	Teleostei			6.3**	S > W, P, A		
Mf	Amphipoda					7.2**	A > J, S
	Ofiuroide					4.3*	A > J, S
Pp	Amphipoda			5.0*	W > P, A		
	Brachyura			8.9**	S > W, P, A		
	Caprella					8.4**	J > A
Sr	Decapoda					8.1*	S > J
	Amphipoda	1366.0***	I > M, O				
Ss	Copepoda	5.9**	M > I	5.5**	W, S, A > P		
	Decapoda	5.2*	O > I				
	Mysida	7.1*	M > I, O				
	Ostracoda	7.3*	M > I, O				
	Teleostei	79.3***	I > M, O				

Table 2. Continued

Species	Item	Zones		Seasons		Sizes	
		F	Post-hoc	F	Post-hoc	F	Post-hoc
St	Tanaidacea			4.8*	W > P, S, A		
Sd	Bivalvia					4.9*	A > J
	Caprella	4.5*	O > I, M				
	Ostracoda					4.5*	J > A

Zones: I = inner; M = middle; O = outer. Seasons: A = autumn; P = spring; S = summer; W = winter. Sizes: A = adult; J = juvenile; S = subadult. Species code according to Table 1.

*P < 0.05; **P < 0.01; ***P < 0.001.

gracilicirrus, *Dactylopterus volitans*, *M. americanus*, *Prionotus punctatus*, *Stellifer rastrifer* and *Symphurus tessellatus*) in the winter than in the other seasons, during which a more diversified diet was observed. Only a few species exhibited changes in diet depending on size; namely, *E. argenteus*, which feed mainly on Copepoda as juveniles, and *S. testudineus* which switch from feeding on Ostracoda to Bivalvia as they grow (Table 2).

PERMANOVA analysis, which was used to investigate differences between the pooled items among factors, indicated significant differences in the diet for *Etropus crossotus*, *Harengula clupeola*, *S. rastrifer* and *S. tessellatus* among zones; for *Cathorops spixii*, *H. clupeola* and *P. punctatus* among seasons; and for *Micropogonias furnieri* among size classes (Table 3).

Trophic guilds

For each of the 24 fish species, between 10 and 260 guts were examined. The 24 species were grouped into four different guilds and two isolated species (ANOSIM; $r = 0.849$, $P = 0.001$), although most of these species use more than one item as a main feeding resource (Fig. 2). The first group (1) encompassed the largest number of species and was divided into two guilds (A and B). Guild 1A (Polychaeta eaters) comprised five species, including *Achirus lineatus* (Al), *Trinectes paulistanus* (Tp) and *M. furnieri* (Mf). Guild 1B (Polychaeta/Crustacea eaters) contained eight species, including *Genidens genidens* (Gg) and *E. crossotus* (Ec). Five species, including *Chloroscombrus chrysurus* (Cc) and *S. rastrifer* (Sr), were assigned to the Copepoda guild (2). The Teleostei guild (4) comprised four species including *Trichiurus lepturus* (Tl) and *C. spixii* (Cs). *A. luniscutis* (Au) and *S. testudineus* (Sd) were placed into two separate branches because they had unique diets that included Teleost scales (5) and Bivalvia (3), respectively.

Spatial variation

In the inner zone, fish were categorised, according to dietary composition, into six groups (ANOSIM; $r = 0.949$,

Table 3. Results of PERMANOVA (Pseudo-F) pairwise tests comparing %IRI of postulated feeding groups based on 999 permutations.

Species	Zones	Seasons	Sizes	Zn × Se	Zn × Si	Se × Si
Au	1.11	2.35	1.19	1.74	1.58	1.32
Cp	1.17	2.60*	1.20	1.54	0.87	0.98
Db	4.49	5.85	0.11	2.48	4.00	0.73
Dv	1.41	3.03	1.10	4.11*	0.77	1.02
Ea	2.48	0.55	1.89	0.95	0.54	0.62
Ec	13.78**	3.88	2.18	10.14*	1.55	2.69
Eg	1.45	2.21	2.09	1.93	1.81	0.39
Hc	13.50**	29.67**	3.52	11.57**	3.22	2.76
Ma	1.25	1.24	1.59	0.67	0.50	0.64
Mf	NT	1.49	3.09*	1.50	0.94	0.87
Pp	0.67	2.71*	NT	1.40	0.81	1.19
Sr	5.48**	2.06	0.25	1.89	0.63	1.09
St	4.77*	1.40	1.60	1.59	2.55	2.83

Codes: Zn = zones; Se = seasons; Si = sizes. Species code according to Table 1.

*P < 0.05; **P < 0.01.

$P = 0.001$) (Fig. 3a). The Teleostei guild (1) comprised four species, including *Citharichthys spilopterus* (Cs) and *Cynoscion leiarchus* (Cl). The second group was divided into two guilds. Guild 2A (Crustacea eaters) comprised *S. rastrifer* (Sr) and *D. volitans* (Dv), which fed mainly on Amphipoda and Caprella, whereas guild 2B comprised *S. testudineus* (Sd) and *C. chrysurus* (Cc), which fed mainly on Bivalvia and Ostracoda, respectively. The Polychaeta (3) and Polychaeta/Crustacea (4) guilds encompassed the highest numbers of species, including *E. argenteus* (Ea) and *E. gula* (Eg) in the former, and *E. crossotus* (Ec) and *S. tessellatus* (St) in the latter. Group 5 contained three species that had varied diets consisting mainly of Decapoda, followed by Teleostei and Polychaeta. Group 6 was formed by two species and was divided into two branches, the Teleostei scale (6C) and Copepoda (6D) eaters.

In the middle zone, three groups were formed by cluster analysis (ANOSIM; $r = 0.903$, $P = 0.001$) (Fig. 3b). *S. testudineus* (Sd) and *A. luniscutis* (Au) were placed in two isolated branches. A second group (2) was formed by two guilds. Guild 2B (Crustacea eaters) comprised

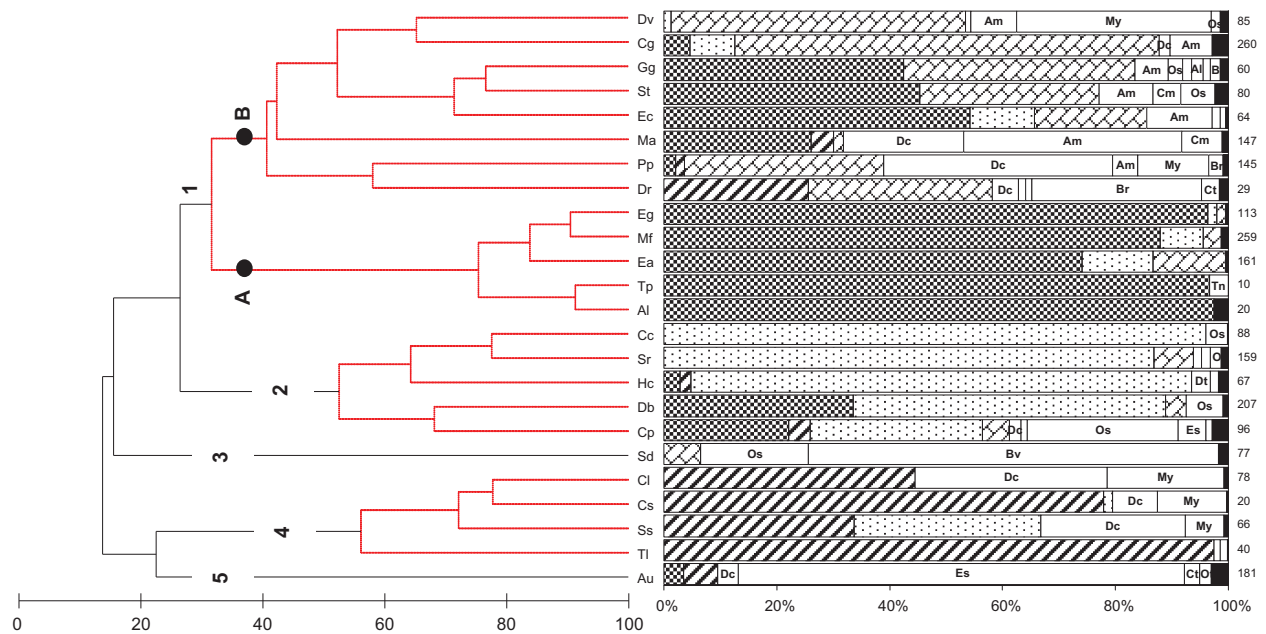


Fig. 2. Composition of main food items according to the index of relative importance (IRI >2%) and dendrogram from the cluster analysis on IRI of 24 fish species from the Sepetiba Bay. [diagonal lines] Caprella; [cross-hatch] Copepoda; [checkered] Polychaeta; [diagonal lines] Teleostei; [solid black] Sum of items with IRI <2%. Number of analysed stomachs containing foods is indicated. Other food items: Al = Algae; Am = Amphipoda; Br = Brachyura; Bv = Bivalvia; Cm = Cumacea; Ct = Teleost crystalline; Dc = Decapoda (shrimp); Dt = Diatomacea; Es = Teleost scale; My = Mysida; Os = Ostracoda; Tn = Tanaidacea. Species code according to Table 1.

S. setapinnis (Ss) and *P. punctatus* (Pp), consuming mainly Decapoda and Mysida. Guild 2C (Teleostei eaters) was formed by four species, among them *Diplectrum radiale* (Dr) and *T. lepturus* (Tl). A third group (3) was formed by 14 species and divided into the following three guilds: 3D (Copepoda eaters), 3E (Polychaeta eaters) and 3F (Crustacea eaters).

Three dietary groups of fishes were identified in the outer zone (ANOSIM; $r = 0.931$, $P = 0.001$) (Fig. 3c). Group 1 consisted of a large number of species (16 species) and had three guilds. Guild 1A (Copepoda eaters) had four species, including *H. clupeola* (Hc) and *S. rastriifer* (Sr), and guilds 1C (Crustacea eaters) and 1D (Polychaeta/Crustacea eaters) had three and eight species, respectively. An isolated branch (1B) comprised *S. testudineus* (Sd), which fed mainly on Caprella and Bivalvia. Groups 3 and 4 had varied diets, feeding mainly on Teleostei, Mysida and Decapoda, and Teleost scales, Polychaeta, Algae, Teleostei and Teleost crystalline, respectively.

The highest within-group average similarities were found for the Polychaeta (G3, 91.03%) and Teleostei (G1, 77.81%) guilds in the inner zone, and for the Teleostei/Crustacea (G2-B, 74.56%), Polychaeta/Crustacea (G3-E, 70.89%) and Copepoda (G3-D, 70.85%) guilds in the middle zone (Table 4). In the outer zone, the Teleostei/Crustacea guild (G2, 69.7%) had the highest within-group average similarity.

Seasonal variation

Three groups were formed by cluster analysis during the winter (ANOSIM; $r = 0.949$, $P = 0.001$) (Fig. 4a). Group 1 was formed by *S. testudineus* (Sd), which had a unique diet consisting of Bivalvia and Ostracoda, and *C. chrysurus* (Cc), which fed on Ostracoda and Caprella. Group 2 (Polychaeta/Crustacea guild) was formed by 13 species, including *D. rhombeus* (Db), *M. furnieri* (Mf) and *S. rastriifer* (Sr). Group 3 was divided into two isolated branches, composed of *A. luniscutis* (Au) and *D. radiale* (Dr), and one guild (Teleostei eaters) that included four species.

In the spring, four groups were defined, according to cluster analysis (ANOSIM; $r = 0.920$, $P = 0.001$) (Fig. 4b). Group 1 was formed by four species. Guild 1B (Teleostei eaters) included three species, whereas guild 1A contained only *A. luniscutis* (Au). Groups 2 and 3 were each formed by only one species that fed mainly on Bivalvia (*S. testudineus*, Sd) and on Mysida (*D. radiale*, Dr), respectively. Group 4 was formed by three guilds and included the highest number of species. Guild 4C (Polychaeta eaters) consisted of eight species, whereas guilds 4D (Caprella eaters) and 4E (Copepoda eaters) contained only three and four species, respectively.

In the summer, two groups were formed by cluster analysis (ANOSIM; $r = 0.888$, $P = 0.001$) (Fig. 4c). Group 1 included *A. luniscutis* (Au) and the Teleostei

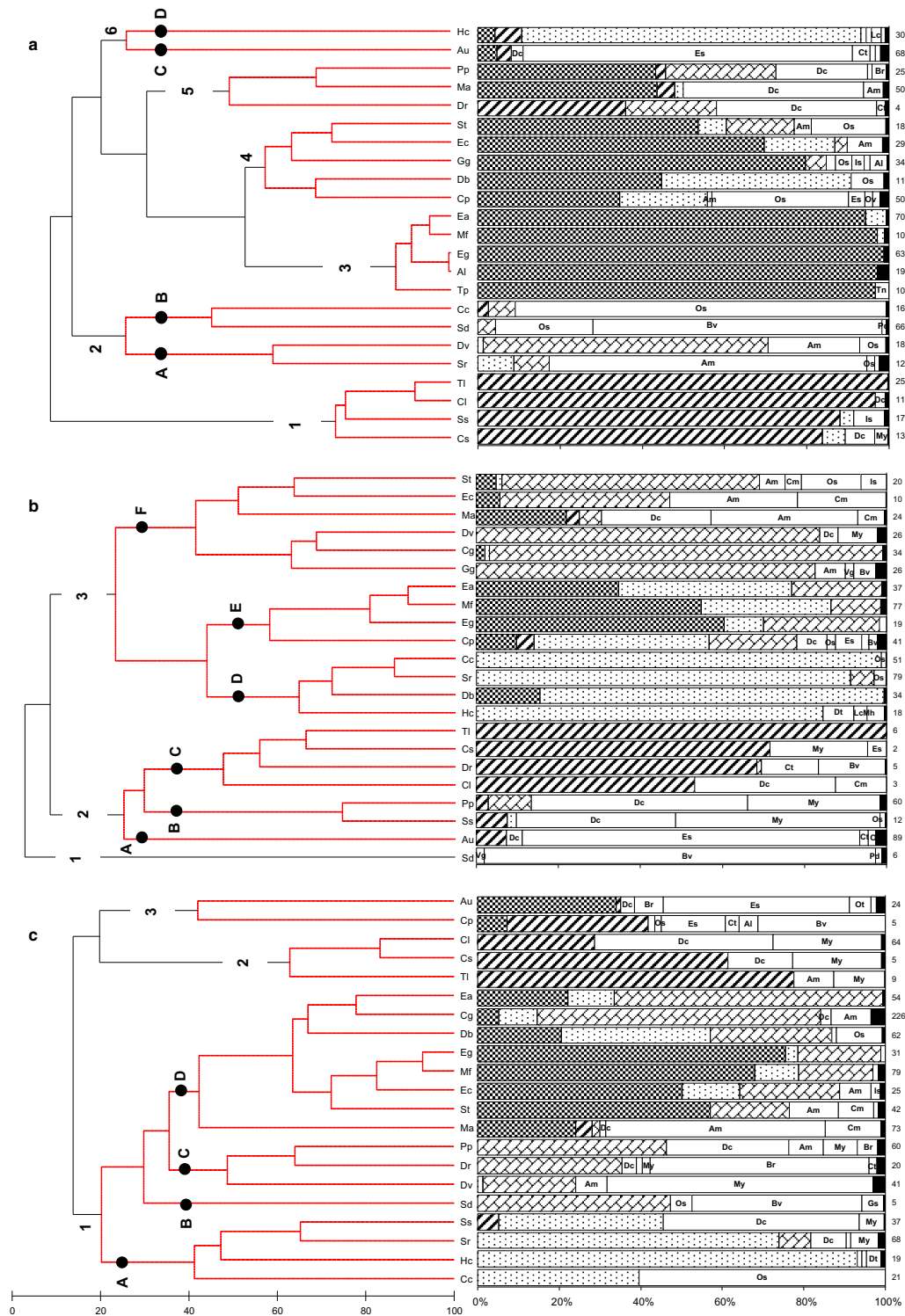


Fig. 3. Composition of main food items according to the index of relative importance (IRI > 2%) and dendrogram from the cluster analysis on IRI of fish species from the zones (a: inner; b: middle; c: outer) of Sepetiba Bay. ▣ Caprella; ▤ Copepoda; ▥ Polychaeta; ▦ Teleostei; ■ Sum of items with IRI < 2%. Number of analysed stomachs containing foods is indicated. Other food items: Al = Algae; Am = Amphipoda; Br = Brachyura; Bv = Bivalvia; Cm = Cumacea; Ct = Teleost crystalline; Dc = Decapoda (shrimp); Dt = Diatomacea; Es = Teleost scale; Gs = Gastropoda; Is = Isopoda; Lc = Cirripedia larvae; Mh = unidentified item; My = Mysida; Os = Ostracoda; Ot = Teleost bone; Ov = Teleost egg; Pd = Rock; Tn = Tanaidacea; Vg = plant. Species code according to Table 1.

Table 4. Summary results of the similarity percentage analysis (SIMPER) of the contribution of food types to the formation of trophic guilds in the three zones of Sepetiba Bay. Items contributing 90% to the average similarity are listed. Average similarity within the guilds (in parentheses) and % contribution of each item are indicated.

Inner			Middle			Outer		
Guild	Food types	%	Guild	Food types	%	Guild	Food types	%
G1 (77.81)	Teleostei	94.94	G2-C (53.54)	Teleostei	100.0	G2 (69.70)	Teleostei	54.41
							Mysida	34.28
							Decapoda	11.3
G4 (62.07)	Polychaeta	56.63	G3-E (70.89)	Polychaeta	36.78	G1-D (62.34)	Polychaeta	40.83
	Copepoda	17.85		Copepoda	33.18		Caprella	34.41
	Ostracoda	13.07		Caprella	30.04		Copepoda	13.08
	Amphipoda	6.70					Amphipoda	10.17
G2-A (59.98)	Amphipoda	46.56	G3-F (48.91)	Caprella	72.83	G1-C (53.84)	Caprella	51.18
	Caprella	28.93		Amphipoda	12.74		Mysida	18.87
	Ostracoda	13.56		Polychaeta	7.85		Amphipoda	17.09
	Copepoda	10.94					Brachyura	6.92
G5 (56.68)	Decapoda	47.74	G2-B (74.56)	Decapoda	45.79	G3 (42.05)	Teleost scale	39.80
	Polychaeta	19.39		Mysida	41.73		Polychaeta	27.10
	Teleostei	15.59		Teleostei	12.48		Algae	12.04
	Teleostei egg	14.08					Teleostei	10.99
							Teleost crystalline	10.06
G2-B (46.18)	Ostracoda	70.14	G3-D (70.85)	Copepoda	97.93	G1-A (47.29)	Copepoda	89.44
	Caprella	29.86					Decapoda	5.76
G3 (91.03)	Polychaeta	98.76						

guild (1B), which comprised four species. Group 2 comprised 18 species divided into three guilds. Guild 2C (Polychaeta eaters) was formed by four species, and guilds 2D (Copepoda eaters) and 2F (Crustacea eaters) were formed by seven and four species, respectively. An isolated branch (2E) was formed by *S. testudineus* (Sd), which fed mainly on Bivalvia and Ostracoda.

Seven groups were formed by cluster analysis during autumn (ANOSIM; $r = 0.923$, $P = 0.001$) (Fig. 4d). Groups 1 and 2 were each formed by only one species, *S. testudineus* (Sd) and *A. luniscutis* (Au), which fed mainly on bivalves and teleosts, respectively. Guilds 3 (Teleostei/Crustacea eaters) and 4 (Copepoda eaters) had five and four species, respectively. Guilds 5 (Polychaeta eaters) and 6 (Polychaeta/Crustacea eaters) had five and two species, respectively. Guild 7 (polychaete and caprellid eaters) was formed by five species, including *C. gracilicirrhus* (Cg) and *M. americanus* (Ma).

No consistent average similarities (>70%) were detected in the winter (Table 5). The highest within-group average similarity was obtained by the Teleostei guild in the spring (G1-B, 73.68%), and by the Polychaeta guild in the summer (G2-C, 77.13%) and autumn (G5, 84.19%).

Size variation

Two dietary groups were formed for the juvenile fish, according to cluster analysis (ANOSIM; $r = 0.908$,

$P = 0.001$) (Fig. 5a). Group 1 comprised 17 species and was divided into three guilds. Guild 1B (Copepoda eaters) was formed by three species, and guilds 1C (Polychaeta and Copepoda eaters) and 1D (Crustacea eaters) were formed by eight and five species, respectively. An isolated branch (1A) was formed by *S. testudineus* (Sd), which fed mainly on Ostracoda, caprellids and Bivalvia. Group 2 was formed by six species and divided into two guilds. Guilds 2F (Teleostei/Crustacea eaters) and 2G (Teleostei eaters) had only three and two species, respectively. *A. luniscutis* (Au) was placed in an isolated branch (2E).

Four groups were formed by subadults, according to the cluster analysis (ANOSIM; $r = 0.952$, $P = 0.001$) (Fig. 5b). Group 1 comprised *S. testudineus* (Sd), which fed mainly on Bivalvia. Group 2 was formed by the Copepoda guild (2B), containing three species, and *C. spixii* (Cp), which fed on a varied diet consisting mainly of Ostracoda, Copepoda and Polychaeta. Group 3 comprised 13 species and was divided into two guilds, namely, Polychaeta eaters (3C) and Crustacea eaters (3D). Group 4 was formed by two isolated species, *A. luniscutis* (Au) and *P. punctatus* (Pp), and the Teleostei guild (4G).

Cluster analysis for adults yielded five groups (ANOSIM; $r = 0.952$, $P = 0.001$) (Fig. 5c). Groups 1 and 2 were each formed by one species, *S. testudineus* (Sd) and *D. radiale* (Dr), which fed mainly on Bivalvia and Brachyura, respectively. Group 3 corresponded to the

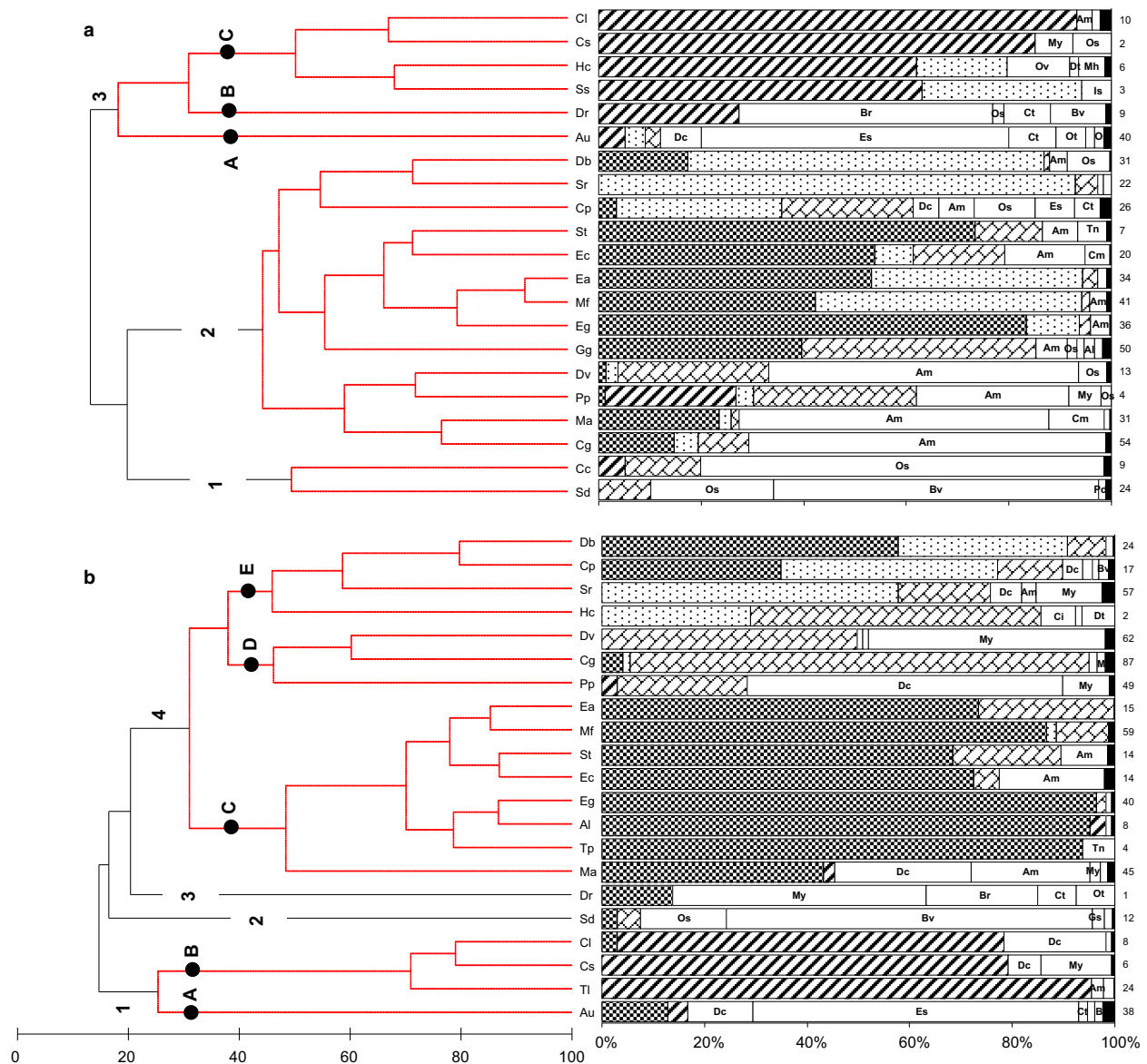


Fig. 4. Composition of main food items according to the index of relative importance (IRI > 2%) and dendrogram from the cluster analysis on IRI of fish species in the seasons (a: winter; b: spring; c: summer; d: autumn). ▨ Caprella; ▩ Copepoda; ▤ Polychaeta; ▧ Teleostei; ■ Sum of items with IRI < 2%. Number of analysed stomachs containing food is indicated. Other food items: Al = Algae; Am = Amphipoda; Br = Brachyura; Bv = Bivalvia; Ci = Cirripedia; Cm = Cumacea; Ct = Teleost crystalline; Dc = Decapoda (shrimp); Dt = Diatomacea; Es = Teleost scale; Gs = Gastropoda; Is = Isopoda; Lc = Cirripedia larvae; Lp = Polychaeta larvae; Mh = unidentified item; My = Mysida; Os = Ostracoda; Ot = Teleost bone; Ov = Teleost egg; Pd = Rock; Tn = Tanaidacea; Vg = plant. Species code according to Table 1.

Teleostei guild (3B) and *A. luniscutis* (Au). Group 4 contained only *M. furnieri* (Mf), which fed mainly on Amphipoda and Ophiuroidea. Group 5 comprised 14 species and was divided into the Copepoda guild (5C) and the Polychaeta/Crustacea guild (5D).

The highest within-group average similarities were found for the Copepoda guild in the juvenile (G1-B, 72.73%) and subadult (G2-B, 73.14%) fish, and for the Teleostei/Crustacea guild in the juveniles (G2-F, 73.69%).

Among the adults, the Teleostei guild (G3-B, 80.77%) had the highest within-group similarity (Table 6).

The relative importance of the three feeding dimensions, as determined using the RELATE routine, yielded trends with significant correlations between all pairwise comparisons. The highest Kendall's rank correlation coefficients were found between sizes ($SL_1 \times SL_2 = 0.60$; $SL_1 \times SL_3 = 0.42$; $SL_2 \times SL_3 = 0.54$) and the lowest between zones (inner \times middle = 0.40; inner \times outer =

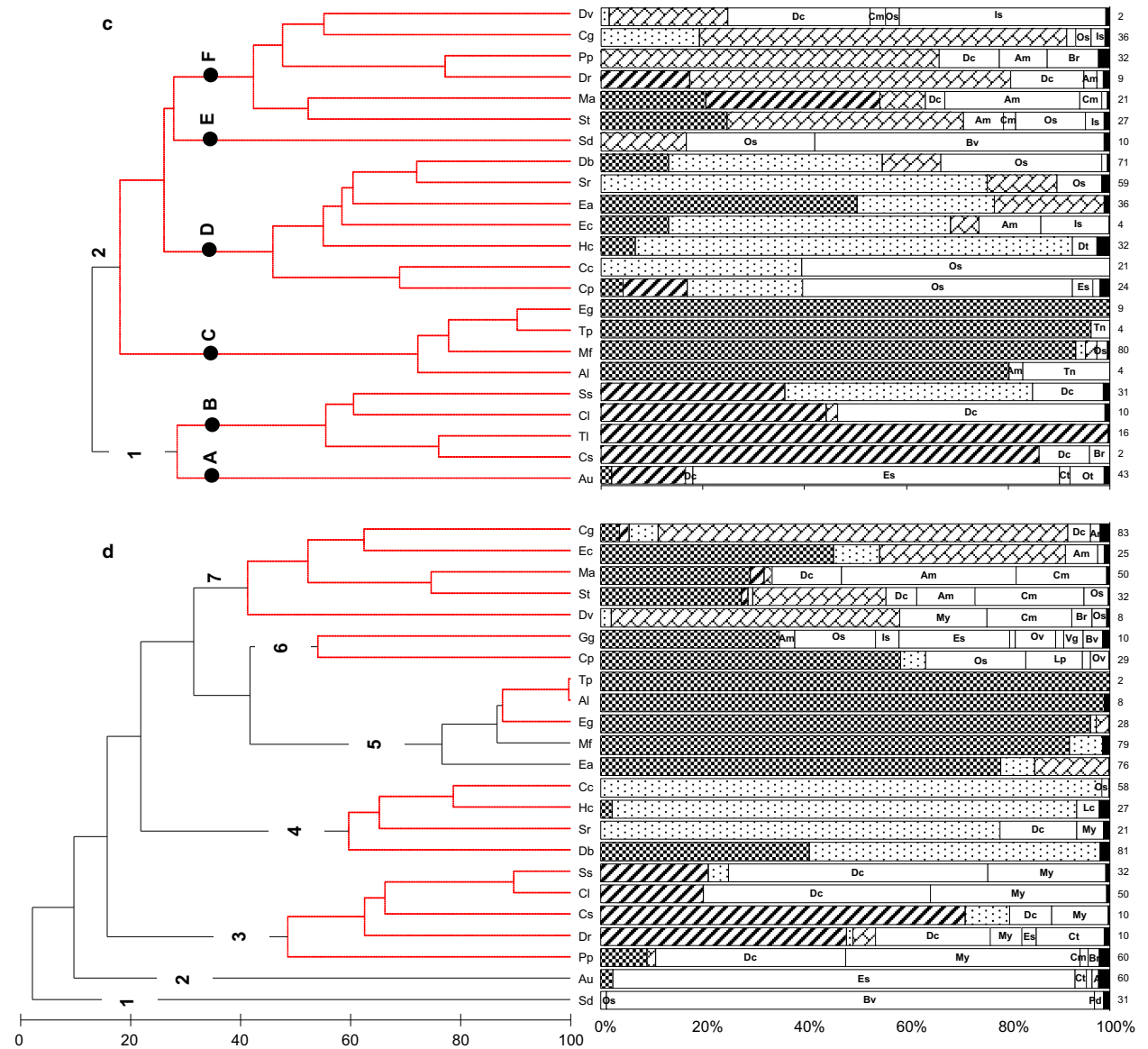


Fig. 4. Continued

0.31; middle \times outer = 0.34), with the seasonal changes showing intermediate values.

Discussion

Diet and trophic guild

Five trophic guilds and two species with differentiated feeding habits were recurrent in the three examined dimensions for the 24 dominant fish species in Sepetiba Bay. Although the aim of this paper was not to provide a rigorous classification scheme of trophic guilds, our findings will facilitate reliable quantitative comparisons

between typical species of estuarine ichthyofauna with different regions. The identification of guilds provides a simple means of reducing complex food webs into tractable components by delineating species that are both functionally similar and possess higher potential for interspecific interactions (Reum & Essington 2008). Elliott *et al.* (2007) identified seven broad categories, but only four groups (zoobenthivore, zooplanktivore, piscivore, and miscellaneous/opportunist) correspond to the results of this study, which described five guilds (Polychaeta, Copepoda, Teleostei, Teleostei/Crustacea and Polychaeta/Crustacea). Similar to Hajisamæ (2009), we failed to identify herbivorous and omnivorous groups, which

Table 5. Summary results of the similarity percentage analysis (SIMPER) of the contribution of food types to the formation of trophic guilds for each season. Items contributing 90% to the average similarity are listed. Average similarity within the guilds (in parentheses) and % contribution of each item indicated.

Winter			Spring			Summer			Autumn		
Guild	Food types	%	Guild	Food types	%	Guild	Food types	%	Guild	Food types	%
G3-C (56.66)	Teleostei	92.97	G1-B (73.68)	Teleostei	81.71	G1-B (59.77)	Teleostei	82.02	G3 (60.47)	Decapoda	38.55
				Mysida	10.88		Decapoda	17.98		Mysida	31.07
G2 (52.02)	Polychaeta	31.07	G4-C (68.21)	Polychaeta	84.81	G2-C (77.13)	Polychaeta	96.87	G5 (84.19)	Polychaeta	94.56
				Caprella	8.48		G6 (54.10)	Polychaeta		45.29	
				Amphipoda	23.21			Ostracoda		30.45	
				Caprella	21.35			Teleost egg		14.59	
G1 (50.15)	Caprella	39.36	G4-D (50.91)	Caprella	69.43	G2-F (47.60)	Caprella	56.40	G7 (51.17)	Caprella	37.64
				Mysida	22.20		Decapoda	15.57		Polychaeta	19.63
G4-E (55.85)	Copepoda	52.42	G4-E (55.85)	Copepoda	52.42	G2-D (53.15)	Copepoda	64.22	G4 (64.74)	Copepoda	97.19
				Caprella	29.95		Ostracoda	13.90			
				Polychaeta	9.01		Polychaeta	13.15			
				Amphipoda	9.13		Amphipoda	11.34			
				Isopoda	3.58		Cumacea	10.69			
G4-F (55.85)	Copepoda	52.42	G4-F (55.85)	Copepoda	52.42	G4-F (55.85)	Copepoda	64.22	G4 (64.74)	Copepoda	97.19
				Caprella	29.95		Ostracoda	13.90			
				Polychaeta	9.01		Polychaeta	13.15			

could be attributed to the lack of vegetation from which herbivorous and omnivorous species incorporate plants, algae or macrophytes.

The composition of the diets of all examined fishes indicates that they were carnivorous and adopted different feeding strategies; however, only six main food types were found to be of particular importance, namely, Polychaeta, Teleostei, Copepoda, Caprellidae Amphipoda, Bivalvia and Teleostei. Polychaeta was the most important food source, particularly in the inner zone, where it was either the major or a supplementary food source for at least 12 species. *A. lineatus*, *Trinectes paulistanus*, *Eucinostomus argenteus*, *Eucinostomus gula* and *M. furnieri* were categorised in the Polychaeta guild, although the latter three species shifted diets according to zone (*E. argenteus* and *E. gula*) and size class (*E. argenteus* and *M. furnieri*). The consumption of Polychaeta by these species has been reported in the recent literature (Derrick & Kennedy 1997; Munroe 2002; Figueiredo & Vieira 2005; Corbisier *et al.* 2006; Mendoza-Carranza & Vieira 2008).

According to Pianka (1980), there is competition among guild members. By contrast, MacNally (1983) reported that one should not assume competition among members of a guild just because they share the same resources, as guild members may be opportunistically converging on an abundant food resource. This consideration is important because opportunism is quite common in fish (Wootton 1990; Gerking 1994). When a resource

becomes limiting, competing species may specialise according to their species-specific resource preferences, and niche overlap will decrease; however, when resources are extremely limited, competitors may be forced to utilise common resources and niche overlap will consequently increase (Wiens 1993; Gable & Amundsen 2010). Therefore, it is reasonable to suppose that the two Achiridae species, the two Gerreidae species and *M. furnieri* would be potential competitors in the case of a shortage of Polychaeta in Sepetiba Bay because they consistently use this resource as their main food item.

Most fishes in this study fed on more than one food category, reflecting an opportunist behaviour. *E. crossotus*, *G. genidens*, *Menticirrhus americanus*, *Ctenosciaena gracilicirrhus*, *Prionotus punctatus* and *Symphurus tessellatus* fed on Polychaeta and several other items, such as Caprellidae Amphipoda and Decapoda and were classified in the Polychaeta/Crustacea guild. The use of Polychaeta and Crustacea by *C. gracilicirrhus* and *Prionotus scitulus* (congeneric of *P. punctatus*) was reported by Chao (1978) and Ross (1978), respectively. *C. spixii*, *Diapterus rhombeus*, *Harengula clupeola*, *S. rastrifer* and *C. chrysurus* were shown to belong to the Copepoda guild. These species may also feed on other items, such as Ostracoda and Polychaeta, as their diets shift according to zones, seasons and size classes.

Trichiurus lepturus, *Citharichthys spilopterus*, *Cynoscion leiarchus* and *Selene setapinnis* formed the Teleostei guild;

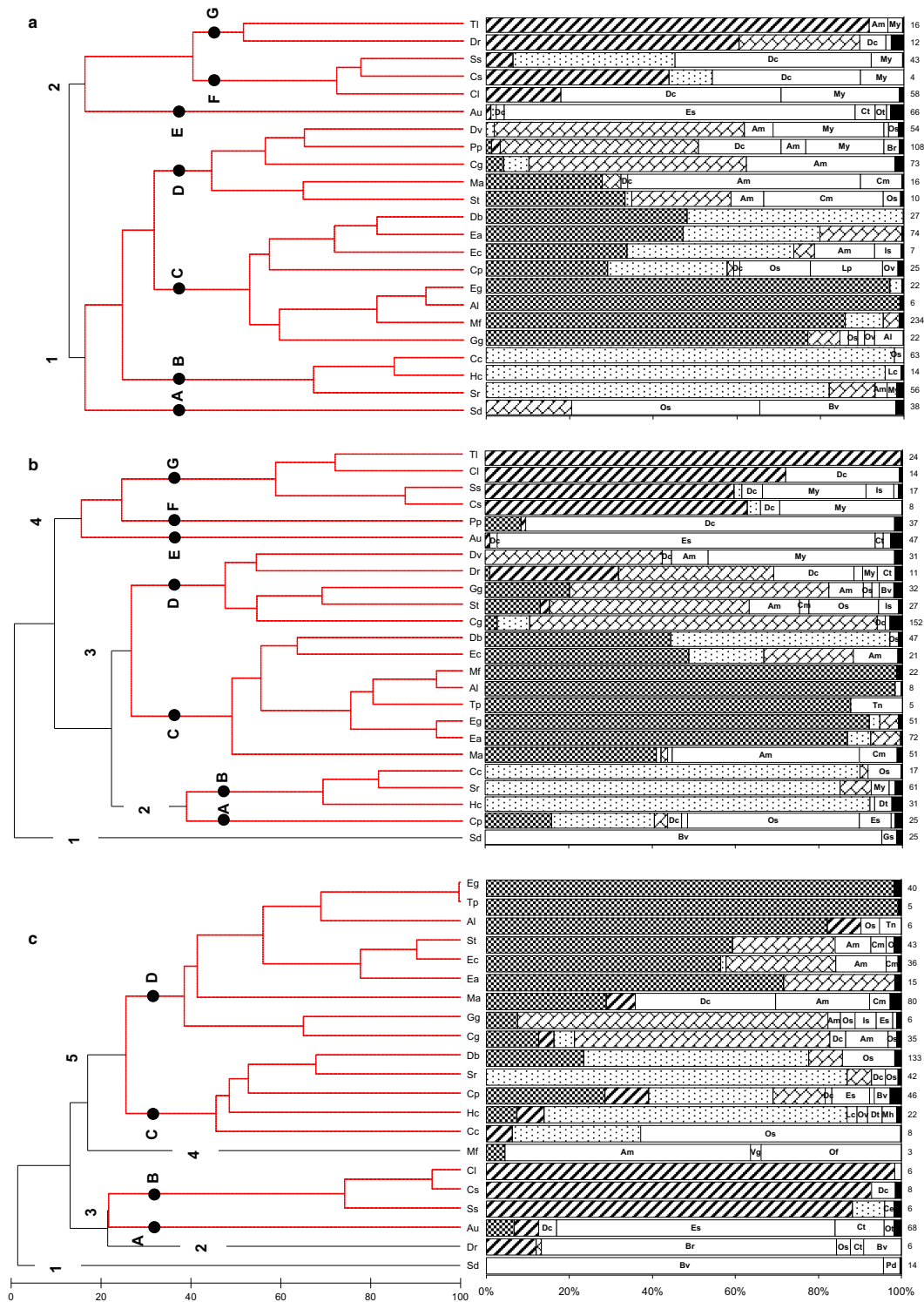


Fig. 5. Composition of main food items according to the index of relative importance (IRI >2%) and dendrogram from the cluster analysis on IRI of fish species in size classes (a: juveniles; b: subadults; c: adults). ▨ Caprella; ▩ Copepoda; ▤ Polychaeta; ▧ Teleostei; ■ Sum of all items with IRI <2%. Number of analysed stomachs containing food is indicated. Other food items: Al = Algae; Am = Amphipoda; Br = Brachyura; Bv = Bivalvia; Ce = Cephalopoda; Cm = Cumacea; Ct = Teleost crystalline; Dc = Decapoda (shrimp); Dt = Diatomacea; Es = Teleost scale; Gs = Gastropoda; Is = Isopoda; Lc = Cirripedia larvae; Lp = Polychaeta larvae; Mh = unidentified item; My = Mysida; Of = Ophiuroidea; Os = Ostracoda; Ot = Teleost bone; Ov = Teleost egg; Pd = Rock; Tn = Tanaidacea; Vg = plant. Species code according to Table 1.

Table 6. Summary results the similarity percentage analysis (SIMPER) of the contribution of food types to the formation of trophic guilds for size classes (SL₁, juveniles; SL₂, subadults; SL₃, adults). Items contributing 90% to the average similarity are listed. Average similarity within the guilds (in parentheses) and % contribution of each item indicated.

Juveniles (SL ₁)			Subadults (SL ₂)			Adults (SL ₃)		
Guild	Food types	%	Guild	Food types	%	Guild	Food types	%
G2-G (51.26)	Teleostei	100.0	G4-G (65.50)	Teleostei	81.46	G3-B (80.77)	Teleostei	95.54
G1-C (59.55)	Polychaeta	73.70	G3-C (62.76)	Decapoda	9.82	G5-D (51.18)	Polychaeta	70.98
	Copepoda	18.82		Polychaeta	88.09		Amphipoda	15.52
G1-D (50.66)	Caprella	43.06	G3-D (51.54)	Copepoda	6.29		Caprella	6.92
	Amphipoda	28.87		Caprella	64.73			
	Polychaeta	12.40		Amphipoda	16.81			
	Cumacea	5.09	Polychaeta	9.68				
	Mysida	4.06						
G1-B (72.73)	Copepoda	100.0	G2-B (73.14)	Copepoda	92.07	G5-C (50.20)	Copepoda	65.64
G2-F (73.69)							Polychaeta	9.54
	Decapoda	47.07					Ostracoda	8.42
	Teleostei	23.31					Caprella	7.79
	Mysida	21.82						

however, several components of Crustacea were also consumed in great amounts by all of these species (with the exception of *T. lepturus*), which in some cases were categorised as the Teleostei/Crustacea guild. Overall, small piscivores use Crustacea as their main food source, switching to piscivory as they grow (Castillo-Rivera *et al.* 2000; Paiva *et al.* 2008). This change is advantageous because fish have a higher energy content (Juanes *et al.* 2002), and crustaceans are more difficult to handle and ingest than fish, resulting in lower capture success, longer handling times and, as a consequence, lower profitability (Juanes *et al.* 2001). Furthermore, in clear water estuaries, piscivores form a major group that hunts their prey visually (Blaber 2000). Low numbers of piscivorous fishes in shallow water have been associated with unfavourable physical conditions (Rozas & Odum 1987; Paterson & Whitfield 2000). The small number of piscivorous species in Sepetiba Bay could be associated, among other constraints, with the low transparency of bay waters, which ranged between 0.3 and 2 m, making searching for and capturing prey more difficult.

Some species used very restricted parts of the available resources irrespective of the three dimensions (spatial, seasonal and size) as in the case of *S. testudineus* and *A. luniscutis*. *S. testudineus* had a differentiated diet consisting mainly of *Bivalvia*. The feeding apparatus of *S. testudineus*, with strong incisors and denticerous plates, and the lack of other similar competitors, may favour specialism in this species that occupies a niche not used

by other species. *A. luniscutis* fed mainly on Teleost scales measuring approximately 8 mm in diameter, which coincided with the findings of Mendoza-Carranza & Vieira (2009) for another marine catfish (*Genidens barbatus*). Teleost scales have been reported to be a component of the diet of juvenile ariids from the neotropics (Hoese 1966; Szelistowski 1989; Chaves & Vendel 1996). Specialism on a particular resource or type of prey is likely to become more effective when a given species forages on a particular niche. According to Leonardos (2008), when a species specialises on a particular type of prey, it may be less able to feed effectively on other prey, especially if the required foraging skills vary between different prey types.

The five trophic guilds and two species with specialised feeding habits appear to be the strategies used by fishes in Sepetiba Bay to partition the available resources, mainly Polychaeta and Crustaceans. This information is fundamental for understanding the complex associations of fishes and fish communities and for identifying groups of species that use similar resources. However, the full utility of this approach will be better realised when food habit data, spanning several years, are available to obtain a better and more robust picture of the fish functional groups and their roles in assemblage organisation.

Spatial, seasonal and size variations

Spatial changes in resource use by the ichthyofauna in Sepetiba Bay appeared to be an important mechanism for

sharing the available feeding resources. Overall, the majority of species fed on Polychaeta in the inner zone and on Crustacea in the outer zone. Polychaeta have been reported to be an important component of the food web for several demersal and benthic fish associated with sheltered and low turbulence areas (Kawakami & Amaral 1983; Schafer *et al.* 2002; Serrano *et al.* 2003). The inner zone of Sepetiba Bay is sheltered, which favours the sedimentation of suspended matter and the formation of a muddy substratum (Araújo *et al.* 2002). Wildsmith *et al.* (2005) reported that filter feeders and burrowing Polychaeta have an affinity for habitats of low wave dynamism, with a high suspended organic matter availability for these species. Moreover, the use of Polychaeta as food by some species in the outer bay zone indicates a wide distribution of this resource throughout the bay, as well as its importance as a major food item to support the ichthyofauna.

The Achiriidae (*A. lineatus* and *T. paulistanus*) are species that use estuarine and low salinity areas as reproduction and rearing grounds (Miller *et al.* 1991; Allen & Baltz 1997; Walsh *et al.* 1999). *A. lineatus* and *T. paulistanus* coexist in the inner bay zone (Guedes & Araújo 2008), where they efficiently exploit Polychaeta and tolerate the environmental changes typical of inner zones, taking advantage of available resources that seem to be abundant. By contrast, some species, such as *C. chrysurus*, despite occurring mainly in the inner bay zone (Azevedo *et al.* 2006), did not use Polychaeta as the main food source, but fed mainly on Copepoda and Ostracoda instead. Despite being a bottom dweller, *C. chrysurus* efficiently uses the water column and feeds on components of plankton. Another major species that feeds on plankton is *H. clupeiola*, which was the only species that fed mainly on Copepoda across the three bay zones, although PERMANOVA detected changes in secondary food items across the zones. This species is a major filter feeder in the bay and plays a very important role in energy transfer from copepod zooplankton to higher levels of the food web. Clupeids function as a major trophic link in bay food chains via their role in converting planktonic biomass into forage for piscivorous fishes. In Sepetiba Bay, the planktonophagous *H. clupeiola* and the Polychaeta feeder *M. furnieri* are among the fish most often consumed by Teleost feeders. The latter species is very abundant in the bay and plays an important role in energy transfer, due to its consumption of detritivore-consuming prey, such as Polychaeta and Crustacea.

The marine catfish from the Ariidae family, *A. luniscutis*, *C. spixii* and *G. genidens*, are commonly associated with inner bay and estuarine zones (Barletta *et al.* 2008). In Sepetiba Bay, these species had different feeding habits; *G. genidens* and *C. spixii* are both strongly associated with the inner zone and feed mainly on Polychaeta and on

Polychaeta and Ostracoda, respectively. *A. luniscutis* is a marine catfish that is widely distributed throughout the bay and has a specialised diet of Teleost scales across the three zones. Although an overlap in diet is expected for closely related species, such as marine catfish, trophic partitioning was observed. Marine catfish have a different buccal apparatus and other morphological constraints that enable diet partitioning, as reported by Araújo (1984). Blaber *et al.* (1994) found a close relationship between diet and dentition in tropical ariid catfish, with strong relationships between dietary guild and the size and arrangement of the palatine teeth. In the present study, an overlap the diet of these species is likely reduced by differential distribution patterns within the bay area.

Nine of the 24 examined species use Polychaeta as a main food source in both spring and autumn, which suggests that Polychaeta peak in abundance during these seasons. Although there is no information available on the reproductive period of Polychaeta in this area, other studies in Southern Brazil have reported reproductive peaks in autumn and winter (Santos 1994; Souza & Borzone 2000). According to MacCord & Amaral (2007), there is a tendency for an extended reproductive period in warmer areas. Seasonal convergence in diet during periods of high prey abundance has been noted in other communities (Pianka 1980; Farias & Jaksic 2007) and suggests opportunistic feeding during periods of prey abundance. Conversely, the greatest dietary diversity observed in a given season could be attributed to decreases in the availability of a particular prey, which would force predators to switch to another type of prey that might be readily available (Leonardos 2008). Changes in use of the preferred food item were found in at least one season for 13 species (*C. chrysurus*, *C. leiarchus*, *S. setapinnis*, *C. gracilicirrhus*, *C. spixii*, *D. rhombeus*, *D. volitans*, *E. crossotus*, *G. genidens*, *H. clupeiola*, *M. americanus*, *P. punctatus* and *S. tessellatus*); changes in the last 11 have been confirmed by ANOVA, indicating a great degree of opportunism in response to changes in prey availability. By contrast, the following eight species consistently used a given resource throughout all seasons: *S. testudineus* (Bivalvia); *T. lepturus* and *C. spilopterus* (Teleostei); *A. lineatus*, *T. paulistanus* and *E. gula* (Polychaeta); *A. luniscutis* (Teleostei scale); and *S. rastrifer* (Copepoda). The last two species, however, showed significant seasonal differences, according to ANOVA, due to changes in secondary food items. Seasonal changes in diet have been reported elsewhere and attributed mainly to prey availability and vulnerability (Akin & Winemiller 2006; Reum & Essington 2008), the competitive capacity of predators (exploitation *versus* interference competition) and environmental constraints (Xie *et al.* 2000; Stoner 2004). Reasons for seasonal changes in diet are unclear, and further studies are needed

to understand the mechanisms behind such changes. It is difficult to predict resource availability in Sepetiba Bay because we did not sample feeding resources directly to assess any electivity for those species.

Ontogenetic changes in diet are important in reducing intra- and interspecific competition among fishes (Day *et al.* 1989; Platell *et al.* 1997). Copepoda have been reported as one of the most important feeding items for juvenile fish in coastal and estuarine zones (e.g. Amara *et al.* 2001; Hajisamae & Ibrahim 2008). In this study, only five species (*H. clupeiola*, *S. rastrifer*, *D. rhombeus*, *C. chrysurus* and *E. crossotus*) used Copepoda as a main food item as juveniles and, of those species, the first three continued to use this item in all size classes. Copepoda had the highest within-group average similarity for juvenile fish, whereas Teleostei had the highest similarity for adults. There is a general tendency for marine fish to start as zooplankton feeders, consuming large amounts of calanoid copepods during their young stages, and then to shift to other food sources as they grow (Elliott *et al.* 2002). *Cynoscion leiarchus*, *C. spilopterus*, *M. americanus* and *S. setapinnis* changed diets with size, using items such as smaller-sized Crustacea as juveniles and gradually shifting to larger prey as they grew.

Here, we identified five recurrent trophic guilds in Sepetiba Bay, and the patterns identified in this study represent a baseline that can be compared with other systems, contributing to our knowledge of the trophic ecology of coastal fishes. The fish community changes diet along the spatial, seasonal and size dimensions, displaying species-specific responses to resource availability. At the examined scale, the ichthyofauna seem to change diet more along the spatial and seasonal, than along the size, dimensions, as a result of the differentiated distributions of Polychaeta and Crustaceans. These findings suggest that the different zones of the bay should be better protected to maintain food resources and, consequently, the stability of fish trophic guilds in Sepetiba Bay. Identifying and incorporating information about the bay food web is a first step towards developing management strategies that are sensitive to this particular ecosystem. In addition, policy and restoration measures that are mandated to conform to ecosystem-based management principles can benefit from information on the three dimensions of variability in community level interactions examined in this study.

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