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Trophic organization and functioning of fish populations in the Bay of Guaratuba, Brazil, on the basis of a trophic contribution factor

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Trophic organization and seasonal development in the Bay of Guaratuba (Brazil) are characterized, based on feeding habits of fish species taken from the literature and on a factor that combines biomass and species richness to determine to what extent detritus and primary production contribute to the trophic network. The Bay of Guaratuba contains all trophic categories of fish: herbivores, plankton-eaters, consumers of invertebrates with occasional supplementation of plants and fish, and fish-eaters. Resident and migrant species occupy different trophic ranges, depending on whether their food sources are available on a permanent or seasonal basis. Residents tend to feed on benthic invertebrate meiofauna and macrofauna, using relatively more detritus than primary production sources. Migrants time their presence in the bay with seasonal productivity, especially of plants. Most occasional visitors consume invertebrates plus fish or primarily fish. The fish-eaters could explain the lower number of fish in this estuary in winter. The Trophic Contribution Factor is a useful tool for characterizing the input of basic elements to the trophic network, monitoring how the occupancy status of species affects their time-space variations, and comparing different localities and ecosystems.

Key words: Trophic structure, trophic contribution factor, fishes, estuary, mangrove

INTRODUCTION

Excluding the effects of population movements and variations in abundance, fish species respond to the abiotic cycle in their environment with strikingly constant feeding habits. This fact has often been noted in the ecosystems of mangrove estuaries (KENNISH, 1990; THOLLOT, 1996). In West Africa, LONGHURST (1957) observed a large number of piscivorous species feeding on epifaunal and endofaunal invertebrates. In New Caledonia, THOLLOT (1996) found that detritus-eating species dominate over macro-carnivorous and herbivorous species, a situation also noted by FLORES-VERDUGO et al. (1990) in Mexico. A great many estuary fish species are remarkably adaptable (BOUCHEREAU *et al.,* 1991; BOUCHEREAU, 1994; BOUCHEREAU & GUELORGET, 1998) and opportunistic (ALBARET, 1994) in their feeding habits. So how important are crabs, polychaetes, gastropods and other invertebrate detritus-eaters in relation to

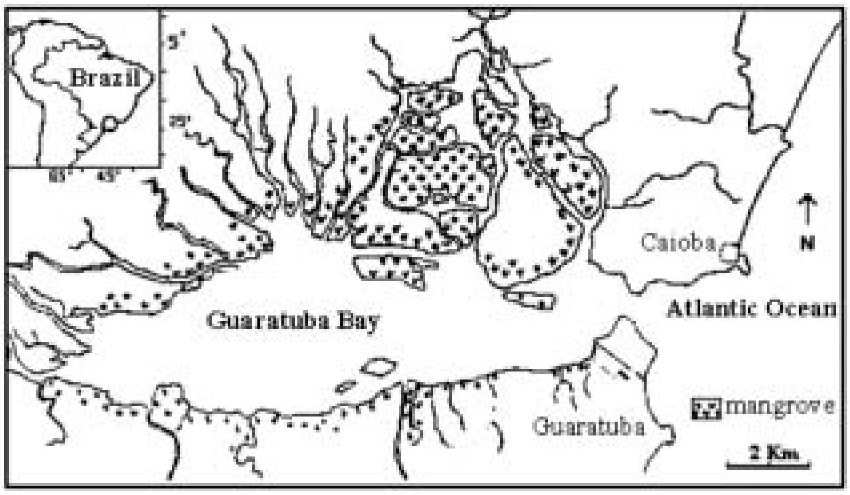

Fig. 1. The Bay of Guaratuba, southern Brazil (in circle in the inset), and the extent of the mangrove

plankton and plants in the diet of fish in a mangrove estuary? Do resident species, migrants and occasional visitors avail themselves of different sources? The aim of this study was to characterize the trophic organization of the permanent and temporary fish populations in the Bay of Guaratuba, Brazil.

The Bay of Guaratuba, southern Brazil (25°52'S; 48°39'W; Fig. 1), is surrounded by a mangrove ecosystem fed by several medium-sized rivers from the surrounding mountains. The estuaries are subject to the abiotic variations common to subtropical paralic environments and the ichthyofauna organization is more affected by the rainfall on the catchment area than by temperature (CHAVES *et al*., 2000). Several ichthyological studies were carried out in Guaratuba to create a database for fish-farming and fish management. They deal with reproductive activity (CHAVES & BOUCHEREAU, 2000) and variations in population numbers (CHAVES & BOUCHEREAU, 1999), showing that most of the fish populations do not permanently live in the bay, but only spend an eco-stage in their life cycle there or enter it sporadically. CHAVES & PICHLER (2000) reported that the trophic activity of fish populations in Guaratuba is more intense in the innermost part of the bay than elsewhere. This activity peaked in autumn and some species changed their diet by targeting other kinds of prey (CHAVES & VENDEL, 1996, 1998; CHAVES & SERENATO, 1998; VENDEL & CHAVES, 1998), evidently due to the availability of different categories of prey as a result of abiotic changes in the estuary.

In this study, the trophic organization is analyzed according to level and feeding habits of the fish populations, based on whether the species is resident, migrant or occasionally visits the bay.

MATERIAL AND METHODS

A quantitative inventory of the ichthyofauna in Guaratuba Bay (CHAVES & BOUCHEREAU, 1999) was made during monthly bottom trawling operations from 1993 to 1996. Sixty-one species were recorded. Information on the diet of 57 of them can be found in the literature. The 57 species can be divided into six groups according to the trophic source consumed, based on an adaptation of the scale used by BOUCHON-NAVARO *et al.* (1992) for West Indian plant bed fish. The six categories are: (I) herbivores that consume algae and higher plants; in the case of grey mullet, a fairly high amount of detritus was found in the stomach; (II) plankton-eaters; (III) omnivores that consume invertebrates of all sizes and plants; (IV) first-order carnivores that consume mostly small benthic invertebrates; (V) second-order carnivores that consume

Table 1. Random values attributed to the factor of trophic usage of the initial energy source in detritus and primary production by each trophic category

Trophic category	Examples of prey composition	Detritus	Primary production
Herbivores	Leaves, seeds, plant debris, aquatic plants	2	2
Plankton-eaters	Phytoplankton and zooplankton	0	2
Omnivores	Polychaetes, mollusks, crustaceans, aquatic plants	2	2
First-order carnivores	Polychaetes, mollusks, crustaceans	2	1
Second-order carnivores	Polychaetes, mollusks, crustaceans, fish	1	0
Fish-eaters	Fish	0	0

mainly invertebrates of all sizes and fish; and (VI) carnivores that consume over 80% fish.

We estimated the proportion of species that belongs to each category and the proportion according to occupancy status (resident, migrant or occasional; QUIGNARD, 1984) which was possible for most of the inventoried species (CHAVES *et al*., 2000; VENDEL & CHAVES, 2001; BOUCHEREAU & CHAVES, 2002). In addition, for the 14 species representing 75% of the total biomass over the study period, we studied the availability of trophic sources in terms of relative biomass by season and occupancy status. Finally, to compare seasons and occupancy status, we quantified the relative amounts of detritus (d) and primary production (pp) used as initial sources (s) of energy in each trophic category (c) by devising a Trophic Contribution Factor (TCF). The TCF for the source in detritus (s = d) or primary production (s = pp) combines biomass or species richness for each trophic category and a usage factor for the initial source of energy (d or pp) used by each trophic category. The TCF can be calculated according to season or occupancy status and is calculated as:

$$TCFs_i = 100 \,.\, \Sigma_{cI \rightarrow cVI} (A_{i,c} \,.\, F_c) \,/\, \Sigma_{i1 \rightarrow in} \Sigma_{cI \rightarrow cVI} (A_{i,c} \,.\, F_c)$$

where i is the season (summer is January-March) or occupancy variable (r for resident, m for migrant, o for occasional), n is the number of units in the variable (i.e., 4 for season and 3 for occupancy status), A is the abundance (density or species richness) in the trophic category (c), and F is the factor of trophic

Table 2. TCF calculation for detritus according to occupancy status; A: hypothetic biomass in each trophic category; F: Factor of trophic usage.

Trophic category	F value for detritus*	Resident		Migrant		Occasional	
		A	AF	A	AF	A	AF
Herbivores	2	8	16	6	12	4	8
Plankton-eaters	0	6	0	5	0	8	0
Omnivores	2	4	8	1	2	10	20
First-order carnivores	2	7	14	4	8	8	16
Second-order carnivores	1	5	5	2	2	10	10
Fish-eaters	0	9	0	2	0	8	0
Total			43		24		54
% of total			35.6		19.8		44.6

* *From Table 1*

usage in each trophic category of the studied source (s), i.e., detritus or primary production. We randomly attributed the values 0, 1 or 2 (Table 1) to the degree of direct contribution of the initial energy source for a trophic category. When members of a category have a very close trophic link to detritus or primary production, the value attributed to F is 2. Conversely, when fish in a category make no direct use of detritus or primary production, the F value is zero. F equals 1 when then a contribution exists but is partial.

TCF values range 0-100. As a theoretical example, we propose that the TCF calculation for comparing the three occupancy statuses according to exploitation of detritus be as shown in Table 2. A similar calculation can be made for primary production.

RESULTS

Proportion of trophic categories

The 57 species for which dietary habits are known feed mainly on invertebrates with or without supplemental plant matter or fish (omnivores, first and second-order carnivores; Table 3). Second-order carnivores is the largest category (38.6%). The second most numerous categories are omnivores (24.6%) and first-order carnivores (19.3%). Only 14% of the species are plankton-eaters (7%) or fish-eaters (7%) and herbivores are the least common (3.5%). Also amongst the 14 species that constitute 75% of the inventoried ichthyofauna abundance, omnivores, first-order and second-order carnivores are most common, followed by fish-eaters (Fig. 2). Herbivores and plankton-eaters are not found in the group of 14.

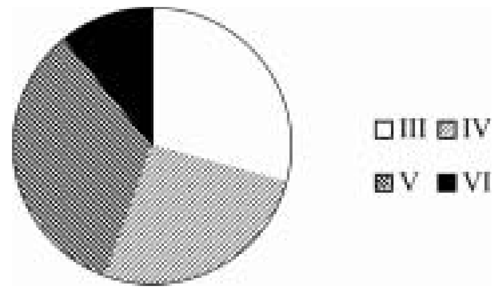

Fig. 2. Relative biomass of the 14 most abundant species in the Bay of Guaratuba, according to trophic category

Table 3. Classification of species for which dietary habits are known into trophic categories. The first 14 constitute 75% of the biomass in the bay, according to samples taken by a benthic trawler

SPECIES	STATUS	REFERENCE	ECOSYSTEM	TROPHIC CATEGORY
Stellifer rastrifer	Resident	Menezes and Figueiredo, 1980	Unspecified	First-order carnivore
		Chaves and Vendel, 1998	Guaratuba	First-order carnivore
Pomadasys covinaeformis	Migrant	Menezes and Figueiredo, 1980	Unspecified	Omnivore
		Costa *et al.,* 1995	North Brazil	Omnivore
		Chaves and Corrêa, 2000	Guaratuba	Omnivore
Bairdiella ronchus	Resident	Menezes and Figueiredo, 1980	Unspecified	Omnivore
		Garcia and Nieto, 1978	Cuba	Omnivore
		Vendel and Chaves, 1998	Guaratuba	Second-order carnivore
Genidens genidens	Resident	Chaves and Vendel, 1996	Guaratuba	Second-order carnivore
Diapterus rhombeus	Migrant	Menezes and Figueiredo, 1980	Unspecified	Omnivore
		Santos and Araujo, 1997	East Brazil	Omnivore
		Chaves and Otto, 1998	Guaratuba	Omnivore
Cynoscion leiarchus	Migrant	Menezes and Figueiredo, 1980	Unspecified	Carnivore
		Chaves and Umbria, 2003	Guaratuba	Carnivore
Isopisthus parvipinnis	Migrant	Menezes and Figueiredo, 1980	Unspecified	Carnivore
		Chaves and Umbria, 2003	Guaratuba	Carnivore
Citharichthys arenaceus	Resident	Chaves and Serenato, 1998	Guaratuba	Second-order carnivore

Table 3. cont`d

Eucinostomus argenteus	Migrant	Menezes and Figueiredo, 1980 Chaves and Otto, 1999	Unspecified Guaratuba	Omnivore Omnivore
Micropogonias furnieri	Migrant	Menezes and Figueiredo, 1980 Chaves and Umbria, 2003	Unspecified Guaratuba	Second-order carnivore Second-order carnivore
Eucinostomus gula	Migrant	Menezes and Figueiredo, 1980 Santos and Araujo, 1997 Chaves and Otto, 1999	Unspecified East Brazil Guaratuba	Omnivore Omnivore Omnivore
Chaetodipterus faber	Migrant	Menezes and Figueiredo, 1985 Hayse, 1990	Unspecified South Caroline, Atl.	First-order carnivore First-order carnivore
Menticirrhus americanus	Migrant	Menezes and Figueiredo, 1980 Chaves and Umbria, 2003	Unspecified Guaratuba	Second-order carnivore Second-order carnivore
Diplectrum radiale	Migrant	Personal observation	Guaratuba	First-order carnivore
Rhinobatos percellens	Occasional	Figueiredo, 1977	Unspecified	First-order carnivore
Gymnothorax ocellatus	Occasional	Randall, 1967 (*G. moringa*)	West Indies	Second-order carnivore
Harengula clupeola	Migrant	Figueiredo and Menezes, 1978	Unspecified	Plankton-eater
Opisthonema oglinum	Migrant	Figueiredo and Menezes, 1978	Unspecified	Second-order carnivore
Pellona harroweri	Migrant	Figueiredo and Menezes, 1978	Unspecified	Plankton-eater
Cetengraulis edentulus	Migrant	Personal observation	Guaratuba	Plankton-eater
Lycengraulis edentulus	?	Figueiredo and Menezes, 1978	Unspecified	Carnivore
Cathorops spixii	Migrant	Figueiredo and Menezes, 1978	Unspecified	First-order carnivore
Netuma barba	Migrant	Figueiredo and Menezes, 1978	Unspecified	First-order carnivore
Sciadeichthys luniscutis	Migrant	Personal observation	Guaratuba	First-order carnivore
Synodus foetens	?	Figueiredo and Menezes, 1978	Unspecified	Second-order carnivore
Hippocampus reidi	?	Personal observation	Guaratuba	Omnivore
Prionotus punctatus	?	Figueiredo and Menezes, 1980	Unspecified	Second-order carnivore
Dactylopterus volitans	?	Figueiredo and Menezes, 1980	Unspecified	Second-order carnivore
Centropomus parallelus	Migrant	Figueiredo and Menezes, 1980	Unspecified	Second-order carnivore
C. undecimalis	Migrant	Figueiredo and Menezes, 1980	Unspecified	Second-order carnivore
Epinephelus itajara	Occasional	Figueiredo and Menezes, 1980	Unspecified	Second-order carnivore
E. niveatus	Occasional	Personal observation	Unspecified	Second-order carnivore
Rypticus randalli	?	Randall, 1967	Puerto Rico	Second-order carnivore
Pomatomus saltator	?	Juanes *et al.*, 1993	South Africa	Second-order carnivore
Caranx hippos	?	Menezes and Figueiredo, 1980 Sierra *et al.*, 1994	Unspecified Cuba	Second-order carnivore Second-order carnivore
C. latus	?	Menezes and Figueiredo, 1980 Sierra *et al.*, 1994	Unspecified Cuba	Second-order carnivore Second-order carnivore
Chloroscombrus chrysurus	Migrant	Menezes and Figueiredo, 1980	Unspecified	Plankton-eater
Selene vomer	Migrant	Personal observation	Guaratuba	First-order carnivore
Trachinotus carolinus	?	Menezes and Figueiredo, 1980	Unspecified	Second-order carnivore
Eucinostomus melanopterus	Migrant	Chaves and Otto, 1999	Guaratuba	Omnivore
Genyatremus luteus	?	Menezes and Figueiredo, 1980	Unspecified	Second-order carnivore
Archosargus rhomboidalis	?	Menezes and Figueiredo, 1980	Unspecified	Omnivore
Cynoscion acoupa	Occasional	Menezes and Figueiredo, 1980	Unspecified	Second-order carnivore
Larimus breviceps	Occasional	Menezes and Figueiredo, 1980 Lopes and Silva, 1999	Unspecified North Brazil	Omnivore Omnivore

Table 3. cont`d

Menticirrhus littoralis	Occasional	Menezes and Figueiredo, 1980 Lunardon, 1990	Unspecified East Brazil	Omnivore Omnivore
Paralonchurus brasiliensis	Migrant	Menezes and Figueiredo, 1980	Unspecified	First-order carnivore
Mugil curema	Migrant	Albaret and Legendre, 1985	Ivory Coast	Herbivore
M. gaimardianus	Migrant	Personal observation	Guaratuba	Herbivore
Bathigobius soporator	Resident	Sano *et al.*, 1984 (*B. fuscus*)	Okinawa Islands	Omnivore
Trichiurus lepturus	Occasional	Figueiredo and Menezes, 2000	Unspecified	Carnivore
Citharichthys spilopterus	Resident	Chaves and Serenato, 1998	Guaratuba	First-order carnivore
Etropus crossotus	Resident	Chaves and Serenato, 1998	Guaratuba	Omnivore
Symphurus tessellatus	Resident	Chaves and Serenato, 1998	Guaratuba	Second-order carnivore
Achirus lineatus	Resident	Chaves and Serenato, 1998	Guaratuba	First-order carnivore
Chylomicterus spinosus	Resident	Personal observation	Guaratuba	Omnivore
Lagocephalus laevigatus	Resident	Personal observation	Guaratuba	Omnivore
Sphœroides testudineus	Resident	Personal observation	Guaratuba	Omnivore

Trophic and occupancy habits

We estimate that 12 of the 57 inventoried species are residents of the bay whereas 25 are migrants, 8 occasional visitors and 12 unknown. For the 45 species whose occupancy is known, invertebrates dominate the diet as all resident and most migrant and occasional species are omnivores, first-order or second-order carnivores (Fig. 3). Herbivores and plankton-eaters were only found in migrant species. Piscivores, absent among residents, were more common in occasional visitors than in migrants (Fig. 3).

No occasional visitors were found among the 14 most abundant species. Amongst the resident species (which correspond to 51% of the biomass of the 14 most abundant species), nearly half the biomass consumes an exclusively invertebrate diet, while the other half feeds on invertebrates plus fish (Fig. 4). Of the migrants (49% of the biomass of the 14 most abundant species), 60% of the biomass feed on invertebrates plus algae and higher plants. Fish capture reaches a fairly highly level, given that fish-eaters account for 20% of the total abundance in this category and second-order carnivores for 10%. Further, the percentage of exclusively invertebrate diets in migrant species is very low (10%) compared to that of residents (45%).

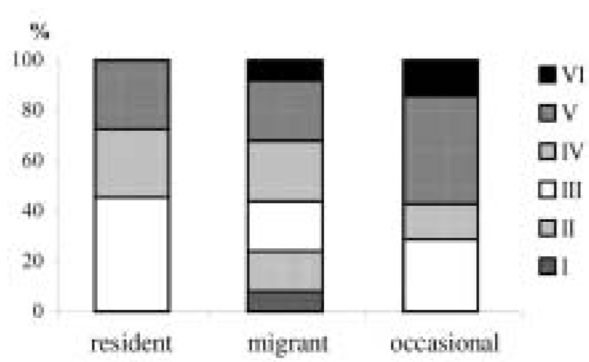

Fig. 3. Distribution (%) of the 45 species in the Bay of Guaratuba, according to occupancy status (resident, migrant, occasional visitor) and trophic category

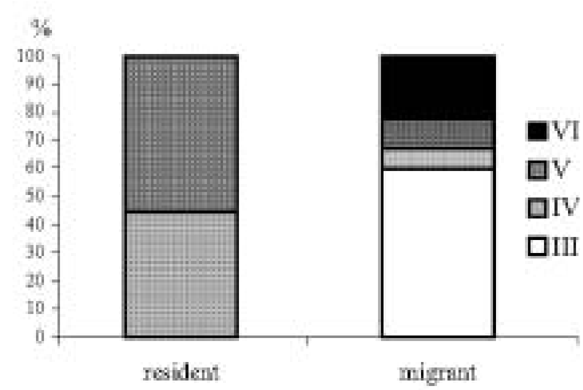

Fig. 4. Distribution (%) of biomass of the 14 most abundant species in the Bay of Guaratuba, according to trophic category

Seasonal variation

Omnivores, first-order and second-order carnivores make up 80% of the biomass of the 14 most abundant species in winter. In other seasons, they make up 91-97% (Fig. 5). Omnivores represent 36% and 39% of the biomass in winter and spring, respectively, while only 11% and 20.7% in summer and autumn, respectively. The biomass of first-order carnivores varies widely depending on the season. It is greater in autumn (54.5%) than during the rest of the year (8.9% in winter, 28.1% in summer).

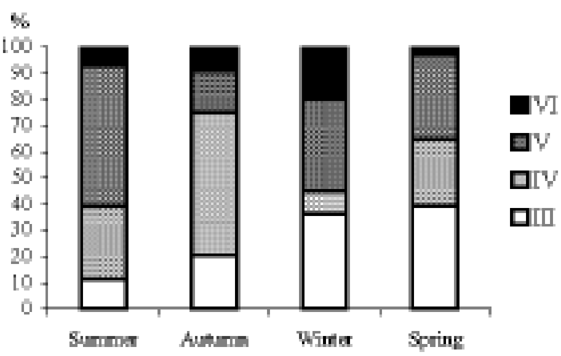

Fig. 5. Seasonal distribution (%) of biomass of the 14 most abundant species in the Bay of Guaratuba, classified by trophic category

Trophic Contribution Factor

For each season, the TCF values for detritus and primary production of the 14 most abundant species do not significantly differ from each other ($X^2 = 0.05$; Fig. 6). Both are lowest in summer (TCFd = 17.1; TCFpp = 11.2) and highest in winter (TCFd = 30.3; TCFpp = 33.8). There are also no significant differences ($X^2 = 0.05$) between TCF detritus and primary production in any season for resident (Fig. 7) and migrant species (Fig. 8) when each occupancy status is examined separately. However, the seasonal trends of detritus and primary production TCF differ according to occupancy status. In resident species, they reach a maximum (TCFd = 33.0; TCFpp = 47.0) in autumn and minimum (TCFd = 18.0; TCFpp = 8.6) in winter, while in migrants, they increase from a minimum (TCFd = 8.4; TCFpp = 7.6) in summer to a maximum (TCFd = 44.0; TCFpp = 43.1) in winter. For the 45 species whose occupancy status is known and regardless of their relative abundance, the detritus TCF is greater than the primary production TCF for residents (d = 34.5; pp = 28.3) and occasional visitors (d = 17.2; pp = 10.9), while the opposite holds for migrants (d = 48.3; pp = 60.9).

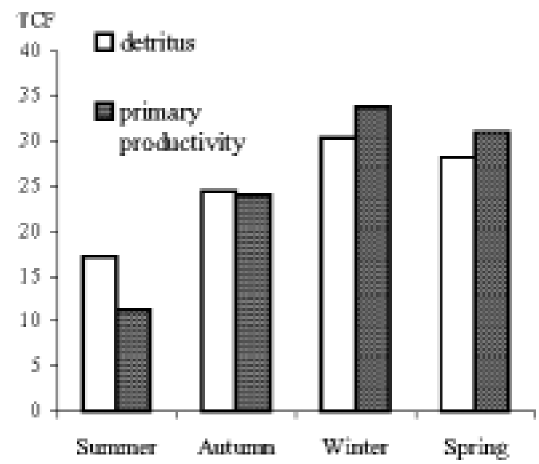

Fig. 6. Seasonal TCF values of detritus and primary production for the 14 most abundant species in the Bay of Guaratuba

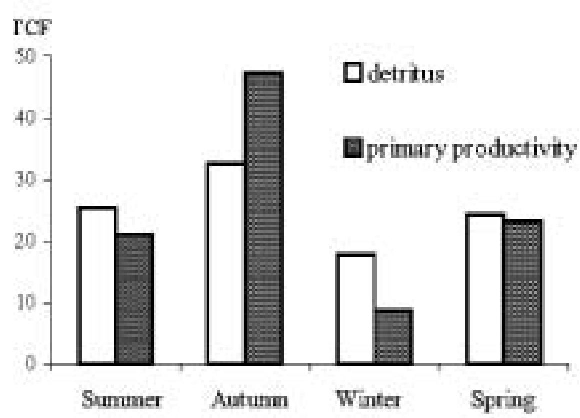

Fig. 7. Seasonal distribution of TCF values of detritus and primary production in resident species in the 14 most abundant species in the Bay of Guaratuba

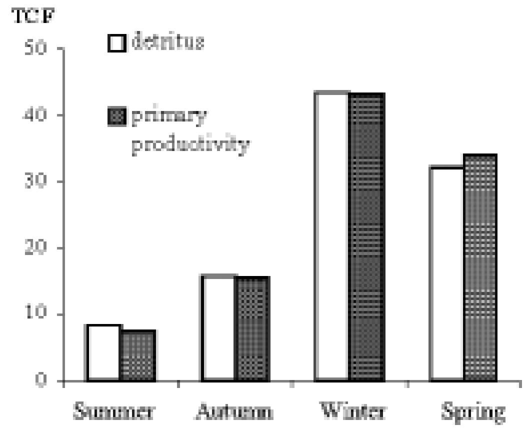

Fig. 8. Seasonal distribution of TCF values of detritus and primary production in migrant species in the 14 most abundant species in the Bay of Guaratuba

DISCUSSION

The dominance of general-diet species with strong carnivorous tendencies (especially invertebrates) over herbivorous or piscivorous species agrees with the findings of studies of other estuary ecosystems (KENNISH, 1990). However, the samples in our study did not involve larval, post-larval and juvenile stages, or fish living in shoreline vegetation zones liable to flooding, which might have restricted the scope of our analysis.

Information on the trophic habits of species with regard to their kind of occupancy illustrates the functional dynamics of the estuary environment, which provides a very hospitable habitat for fishes since all the trophic categories are found there.

Resident species, which feed year-round mainly on a diet of invertebrate benthic meiofauna and macrofauna, profit more from the supply of detritus than the supply of primary production. Their preference for primary production in autumn may be due to the increase in photosynthetic activity at this time of the year. YÁÑEZ-ARANCÍBIA *et al.* (1993) and DUFOUR *et al.* (1994) noted an increase in the phytoplankton biomass in several estuaries when clear waters of marine origin blend with continental waters rich in nutritious salts just after the rainy season. It was also in autumn that this situation was noted in Guaratuba by CHAVES *et al.* (2000). Resident species hold a pivotal position in the trophic network because they are fodder (food web) species in the “energy reactor” and constitute part of the wealth of this type of semi-closed aquatic ecosystem.

Migrants are found in all trophic categories. As they live in the bay during only one eco-stage of their life cycle, they time their presence with the estuary’s seasonal productivity, particularly of the plants consumed by herbivores and plankton-eaters. At the end of the migrants’ food chain, there are fish-eaters that feed not only on fodder species but also on other migrants and occasional visitors.

In occasional visitors, species are present irregularly throughout the year and are most often carnivores and fish-eaters. THOLLOT (1996) showed that, in the New Caledonian mangrove, fish-eaters are more common amongst occasional visitors than among migrants and even more than among residents. They are usually large individuals that wander passively into the bay (BOUCHEREAU *et al.*, 2000) or enter the bay to take advantage of the food supply (CHAVES *et al.,* 1998). Could the relative wintertime increase in fish-eating predators observed in this study explain the decrease in fish numbers in winter, observed by CHAVES & BOUCHEREAU (1999), just after their peak in autumn?

Bay occupancy habits become very clear after determining the seasonal changes in detritus and primary production sources among resident and migrant species. THOLLOT (1996), DIOUF (1996) and others have already noted the important part played by detritus in the trophic network of resident species. Seasonal changes in the biomass of invertebrate eaters are closely related to those of detritus and primary production contribution for residents. In migrants, the same applies to the biomass of invertebrates and plant eaters, which are related to detritus and primary production. We therefore conclude that these two groups of fish avail themselves of different trophic ranges depending on whether the source is available permanently or seasonally.

In this study, the TCF was used to characterize the contribution of the basic elements in the trophic network – detritus and primary production – and examine them in relation to season and occupancy status of the fish species. TCF can also be used to compare locations within an ecosystem or between ecosystems, using the variable *i* as a location in the above formula. Likewise, vertical occupancy (pelagic, demersal or benthic) can be examined. TCF can also be used to examine changes in diet due to the age of the fish, whose biomass in each trophic category can be determined. These examples show how versatile TCF is for analyzing and interpreting trophic organization and functioning in fish populations. However, in a TCF comparison, we may receive varying results for a given location or ecological status, owing to different values assigned to abundance (factor *A*) and use (factor *F*) in the formula. This should be taken into consideration when interpreting TCF results. Another advantage of TCF is that the diet, if already known, can be used to quickly quantify the contribution of energy sources in the environment consumed by fish populations.

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Trofička organizacija i funkcioniranje riblje populacije u zaljevu Guaratuba, Brazil, na osnovi doprinosa trofičkog faktora

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SAŽETAK

U zaljevu Guaratuba je određen trofički sustav i njegov sezonski razvoj. U obzir su uzeti podaci o prehrambenim navikama iz literature kao i jedan faktor koji sjedinjuje biomasu i bogatstvo vrsta kako bi se mogao odrediti doprinos detritusa i primarne proizvodnje u trofičkom lancu. Zaljev ima, s obzirom na ishranu, sve kategorije riba: herbivore, planktonofage, potrošače beskralježnjaka (nadopunom s biljem i ribom), te one koje se hrane ribom. Ribe koje su stalno nastanjene u zaljevu, te migratorne ribe zauzimaju različite trofičke nivoe, ovisno da li su izvori hrane pristupačni stalno ili samo u određenoj sezoni. Stalne vrste se hrane pretežito bentoskim beskralježnjacima (meio - i makrofaunom) te koriste više detritus negoli izvore primarne proizvodnje. Prisustvo migratornih riba ovisno je naročito o sezonskoj biljnoj proizvodnji. Većina povremenih posjetitelja hrani se beskralježnjacima i ribom ili uglavnom ribom. Prisustvo ihtiofaga moglo bi objasniti manje količine ribe zimi u tom zaljevu. Faktor trofičke kontribucije može korisno poslužiti kao prikaz ulaska osnovnih elemenata u prehrambeni lanac i razumijevanju kako zastupljenost vrste utječe na vremensko-prostorne varijacije, te omogućava usporedbu različitih lokaliteta i ekosistema.

Ključne riječi: Trofička struktura, trofički faktor kontribucije, ribe, ušće, mangrove