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ICHTHYOFAUNA IN THE ECOLOGICAL ORGANISATION OF A SOUTH-WEST ATLANTIC MANGROVE ECOSYSTEM: THE BAY OF GUARATUBA, SOUTH EAST BRAZIL

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ICHTHYOFAUNA ORGANISATION FUNCTIONING PARALIC DOMAIN CONFINEMENT ATLANTIC

ICHTYOFAUNE ORGANISATION FONCTIONNEMENT DOMAINE PARALIQUE CONFINEMENT OCEAN ATLANTIQUE ABSTRACT. – The distribution and behaviour of the fish assemblage in the Bay of Guaratuba, an estuarine ecosystem in the south of Brazil, has been studied in different sectors of the bay according to the variety of continental and marine influences they undergo. There are two separate areas in this bay: one primarily of freshwater influence, the other of marine water. Fish are numerically more abundant in the former but the latter is richer in species. It is suggested that other environmental characteristics besides salinity or pH values are important in understanding the organisation and structure of ichthyofauna. The results are related to the concept of confinement in the paralic domain (Guelorget & Perthuisot 1983). In the most confined area under continental influence, species are mostly sedentary, whereas in the area known as marine where the water is more renewed, migrant and sporadic species are largely dominant.

RÉSUMÉ. – L'assemblage de Poissons de la Baie de Guaratuba, un écosystème estuairien du sud du Brésil, a été étudié vis-à-vis de son occupation et de son comportement dans différents secteurs de la baie, en fonction des diverses influences continentale et marine auxquelles il est soumis. Dans cette baie, deux régions s'individualisent: l'une sous influence majeure de l'eau douce, l'autre sous celle de l'eau marine. L'abondance des Poissons est plus grande dans la première région, la richesse spécifique dans l'autre. Il est suggéré que d'autres caractéristiques environnementales que les valeurs de salinité ou de pH sont importantes pour comprendre l'organisation et la structuration de l'ichtyofaune. Les résultats sont mis en relation avec le concept du confinement dans le domaine paralique (Guelorget & Perthuisot 1983). Dans la région la plus confinée, sous influence continentale, les espèces sont dans leur majorité sédentaires. D'autre part, dans la région où l'eau est plus renouvelée, dite marine, ce sont les espèces migratrices et occasionnelles qui dominent en abondance.

INTRODUCTION

With regard to studies carried out in estuarine environments in general, Amanieu & Lasserre (1982) emphasised the part played by research into intra- and inter-species relations between organisms living in these ecosystems rather than more qualitative and quantitative descriptions of their members. An enhanced approach to this idea was proposed by Guelorget & Perthuisot (1983) with the concept of confinement which predicts the distribution of organisms in paralic domains located between marine and continental domains (from Greek: *para*: besides, and *halos*: salt, used by Neuman in 1854) according to gradients extending from the sea up into the estuary. This theory, which is also beginning to find confirmation in the biological subdivision "Fish" (Bouchereau *et al.* 2000a,b,c, Mariani 2001), is especially interesting for two reasons. First because it considers that, at a given point in this ecosystem, it is the rate of renewal in water of marine origin, rather than actual salinity, which determines biological zonation and therefore the composition and organisation of the species and, second, because it can help to understand the organisation of members of whole communities within an ecosystem belonging to the paralic domain. Once the indicator species of more or less confined zones have been defined, estuarine ecosystem management with a view to enhancement can then begin, given that they are not merely extensions of continental or marine domains (Amanieu & Lasserre 1982) but specific ecological units in their own right.

The current study starts from this basis and proposes a typological description, followed by approaches of a functional nature, of the fish community in the Bay of Guaratuba, an estuarine ecosystem in the south of Brazil which is currently the subject of studies on halieutics (local and leisure fishing) and aquaculture. However, work carried out up to now has only involved fish in the mangrove area (about 9 km²) in the zone further north (Chaves & Corrêa 1998, Chaves & Otto 1999, Chaves & Bouchereau 1999, Bouchereau et al. 2000a, Chaves & Bouchereau 2000, Chaves et al. 2000). Even though this research has contributed to knowledge of the migratory, feeding and reproductive habits of the fish populating this part of the bay, no integrating approach has been used so far. In this study therefore, the structure of the ichthyofauna is considered in terms of abundance and diversity in space and time along the sea-continent axis extending across the entire bay, in relation to the abiotic factors of the ecosystem, to clarify whether a biological zonation is consistent with the confinement gradient exits.

MATERIAL AND METHODS

The Bay of Guaratuba $(25^{\circ}52'S; 48^{\circ}39'W)$ covers a surface area of 45 km² surrounded by a wide expanse of mangrove. Monthly series of samples were taken in this area from May 1998 to April 1999, always in the morning. Extra samples were taken in December, breeding season for a great amount of species (Chaves & Bouchereau 2000) to provide further scientific information, making a total of 13 series. Three zones (Fig. 1) were chosen, covering an east-west axis along the bay: zone 1 is the farthest inland and, being located at the mouth of the river Guanxuma, has the highest intake of fresh water; zone 2 is the intermediate zone between zones 1 and 3; zone 3 is close to the mouth at the meeting-point of the bay with the sea.

Temperatures (°C), pH and salinity of surface (for each series) and bottom water (except for the June and October series) were measured in each zone. Pluviometric data from June 1997 to August 1999 were obtained from the SIMEPAR station (the Paraná Meteorology Service) located near the meeting-point, to provide a back record of this variable. To check whether the tide caused a bias for fishing, catch numbers are compared based on tide directions, using the tide tables for the port of Paranaguá, 20 km north of the Bay of Guaratuba.

Two different fishing procedures were applied in each zone: a) a seven-minute trawl by a bottom trawler (stretched 20-mm mesh); b) at 50 to 100 m away from the first to prevent any sampling bias, a catch using a gill net (300 m long, 2 m deep, stretched 70-mm mesh) cast

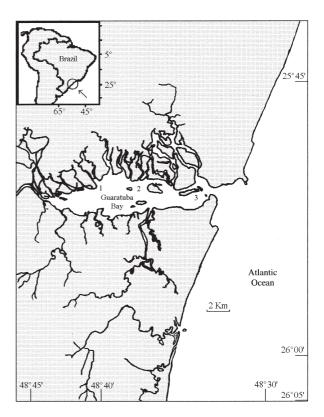


Fig. 1. – The Guaratuba Bay, southern coast of Brazil, and the three zones (1, 2 and 3) of study.

out in an arc of a circle for 30 minutes and reaching the bottom. Each time, to hasten the gilling of fish in the vicinity of the net, the fishermen beat the water surface with oars throughout the operation. Field operations were always carried out in this order: zone 1: a, b; zones 2 and 3: b, a. The fish caught were kept cool until they reached the laboratory where they were identified, counted and weighed (mass M to the decigram).

Abiotic and biotic data series in the three sites were compared by means of Analysis of Variance (ANOVA) and Factorial Correspondance Analysis (FCA). Three tests were used: after verification of the distribution normality, the Fisher test when there were more than two groups/series; the "t" Student test when there were only two (bottom and surface); when distributions were non-normal, the Kruskall-Wallis non-parametric test.

RESULTS

Abiotic data

Spatial analysis: The mean temperature (Fig. 2A) varied from 21.2°C (zone 1) to 23.1°C (zone 3) at the surface and from 23.0°C (zones 1 and 2) to 23.8°C (zone 3) at the bottom. The means were not significantly different for the three zones (Kruskall-Wallis; surface: $X^2=3.56$, degree of freedom df=2, p>0.05; bottom: $X^2=0.71$; df=2; p>0.05).

The mean pH (Fig. 2B, 3A) varied from 6.9 (zone 1) to 7.8 (zone 3) at the surface and from 7.1 (zone 1) to 8.0 (zone 3) at the bottom. It was significantly higher in zone 3 compared to zones 1 and 2, both for water at the surface and at the bottom (Fisher test, F=6.17; df=2; p<0.07 and F=7.23; p<0.05 respectively). The mean surface pH throughout was not significantly different from that at the bottom (zones 1 and 2: Kruskall-Wallis X^2 =0.87 and X^2 =0.61 respectively, zone 3: t-Student: t=0.86; df=1; p>0.05).

The mean salinity (Fig. 2C, 3B) varied from 2.0 (zone 1) to 13.8 (zone 3) at the surface and from 6.5 (zone 1) to 21.8 (zone 3) at the bottom. Surface and bottom salinity were significantly different in the three zones (respectively Kruskall-Wallis, $X^2=13.72$; df=2; p<0.05 and Fisher, F=23.53; df=2; p<0.05). The mean bottom salinity throughout was significantly higher than that of the surface (zone 1: Kruskall-Wallis, $X^2=5.13$; df=1; p<0.05; zone 2:

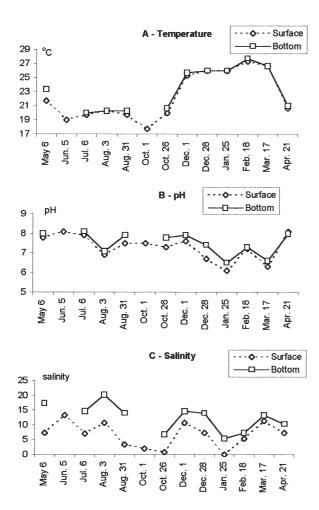


Fig. 2. – Dates of series and surface (s) and bottom (b) values for A: temperature T (°C), B: pH, and C: salinity S according to the zone (1 to 3) and sampling (dates above), in the Bay of Guaratuba from May 1998 to April 1999; X: corresponding means.

Kruskall-Wallis, X²=5.24; df=1; p<0.05; zone 3: t-Student, t=2.75; df=1; p<0.05).

Temporal analysis: The mean water temperature (Fig. 2A) varied from 17.7°C (October) to 27.3°C (February) at the surface and from 20°C (July) to 27.7°C (February) on the bottom. The means were significantly different from one series to another (Kruskall-Wallis, surface: df=12; p<0.05; bottom: df=10; p<0.05). The change in monthly mean variations reveals a warm season at the end of spring and in summer and a cool season in autumn and winter until the start of spring.

The mean pH (Fig. 2B) varied from 6.1 (January) to 8.1 (June and April) at the surface and from 6.5 (January) to 8.1 (July) on the bottom. The means were significantly different from one series to another (Fisher, surface: df=12; p<0.05; bottom: df=10; p<0.05). Monthly changes show minimum values in summer and in August whether the water is at the surface or on the bottom.

Mean salinity (Fig. 2C) varied from 0.0 (January) to 13.3 (June) at the surface and from 5.3 (January) to 20.3 (3^{rd} August) on the bottom. Surface water salinity was not significantly different from one series to another (Kruskall-Wallis: $X^2=15.52$; df=12; p>0.05); at the bottom it was significantly different from other series in November and January (Fisher: F=10.08; df=10; p<0.05).

Rainfall noted in summer (monthly means from 9.3 to 24.8 mm) is higher than that recorded in autumn (monthly means from 1.4 to 5.2 mm) and in other seasons (Fig. 3C).

Biotic data

Species richness: From May 1998 to April 1999, 56 species were caught in all the zones of the Bay of Guaratuba.

Zone 3 was the richest with 41 species altogether, 32 of which were trawled and 22 caught in gill nets (Table I). Zones 1 and 2 were less rich, with a total respectively of 31 and 30, 22 of which were trawled in both zones and 21 (zone 1) and 19 (zone 2) caught in gill nets.

Even though pH is highly dependent on carbonates and the presence of any bacteria, it develops virtually in the same way as salinity and behaves in a similar way with regard to species richness (Fig. 3B, C). The extent of variation in species richness (Fig. 3D) is always higher in zone 3 than in zones 1 and 2. However, variation in species richness does not follow that of gradients in salinity and pH.

Catch numbers: If catch numbers per fishing effort unit are considered in relation to tide direction (Fig. 4A), with the exception of two unusually high

	Zone,	May	Jun	Jul	Aug	Aug	Oct	Oct	Dec	Dec	Jan	Feb	Mar	Apr		
	gear	6	5	6	3	31	1	26	1	28	25	18	17	21		
															*	* *
R	1t	5	3	8	3	7	8	10	9	8	5	5	6	11	22	
	1g	7	3	1	2	3	6	5	7	1	3	1	5	4	21	31
	2t	4	3	3	5	3	5	16	7	6	8	12	6	4	22	
	2g	3	0	1	1	3	4	10	2	5	2	4	5	6	19	30
	3t	3	5	4	3	3	9	25	4	5	15	9	6	5	32	
	3g	1	4	3	4	0	4	14	6	1	6	0	10	5	22	41
																X:
n	1t	163	33	134	6	13	779	233	256	466	101	150	57	156		195.9
	1g	20	3	8	9	8	32	35	16	2	7	1	16	18		13.5
	2t	10	5	15	27	3	5	6	64	10	20	40	15	11		17.8
	2g	5	0	2	1	11	9	46	7	7	3	23	2 6	13		11.8
	3t	7	77	27	299	28	86	81	42	9	68	101	19	7		65.5
	3g	1	5	3	11	0	3	6	12	1	2 6	0	15	5		6.8
	X: t	60.0	38.3	58.7	110.7	14.7	290.0	106.7	120.7	161.7	63.0	97.0	30.3	58.0		-
	g	9	23	4	7	6	15	29	8	3	12	8	19	12		-
М					0.00											X:
	1t	5191	707	2932	97	532	16390	4543	3894	12489	3607	4823	681	2514		4492
	1g	1591	1301	901	1617	797	2622	3585	1900	1068	992	53	1302	1689		1494
	2t	270	74	464	415	69	516	497	1779	263	481	897	392	379		500
	2g	467	0	256	129	1334	1164	5275	946	1638	285	2830	2163	1107		1353
	3t	119	945	359	5080	475	2603	2356	590	239	3865	2613	112	254		1509
	3g	109	451	477	1471	0	714	820	2 618	300	1872	0	1489	594		840
	X: t	1860	575	1252	1864	359	6503	2465	2088	4330	2651	2778	395	1049		-
	g	722	584	545	1072	710	1500	3227	1821	1002	1050	961	1651	1130		-

Table I. – Total catches of fish in number of species (R), number of individuals (n) and mass (M, grams) per sampling and zone, by fishing method: t (trawler) or g (gill net). X: corresponding means.

*: species richness per zone, according to the fishing gear; **: idem, total per zone, both fishing gears.

rising tide values, the tide does not influence catch levels whether it is rising or ebbing.

The total monthly catch (trawler plus gill net) was maximum (914) in October and minimum (63) in August. With the trawler, it was maximum (870) and minimum (44) in the same series; with the net it was maximum in October (87) and minimum in June (8). No statistical difference in mean catches can be seen in separate series (Table I) with the trawler and the gill net (Kruskall-Wallis: both df=12; p>0.05).

Maximum catches with the trawler (2547) and the gill net (175) were in zone 1. Statistically, mean catches (Table I) were significantly different with the trawler from one zone to another, but not with the net (Kruskall-Wallis: both df=2; p>0.05).

Catch in mass: The overall weight of catches observed were maximum in October for a trawl (19751.8 g) and in November for the gill net (9680.5 g). However, means (Table I) do not differ from one series to another either with the trawler or the net (Kruskall-Wallis, both df=12; p>0.05).

Zone 1 had the biggest catch weight whatever the fishing method. Mean catches (Table I) with the trawler were significantly different from one zone to another (Kruskall-Wallis: df=2; p<0.05), but not with the net (Kruskall-Wallis: df=2; p>0.05). Occurrence frequency of species: No species is present in the three zones all year round. The most frequent are Genidens genidens (V.), 92% of the catch in zone 1, Bairdiella ronchus (C.) and Diapterus rhombeus (C.), 85% in zone 2 and Pomadasys corvinaeformis (S.), 62% in zone 3. Eighteen of the species listed (32% of the species richness) have an occurrence of 30% or more (the lower limit arbitrarily defined) in at least one of the three zones studied. According to the trend shown by the occurrence of each species in all three zones (Fig. 4B) and the location of their maximum occurrence, three groups may be distinguished:

I. – Species in the continental area of the bay. Occurrence higher in zone 1 of *B. ronchus, Centropomus parallelus* (P.), *D. rhombeus, G. genidens, Sphoeroides testudineus* (L.), *Stellifer rastrifer* (J.) and *S. tesselatus* (Q. & G.).

II. – Species in the marine area of the bay. Occurrence higher in zone 3 of: *Chlorosombrus chrysurus* (L.), *Cynoscion leiarchus* (C.), *Etropus crossotus* (J. & G.), *Eucinostomus argenteus* (B. & G.), *Mentricirrhus americanus* (L.), *P. corvinaeformis* and *Prionotus* sp.

III. – Species overlapping continental and marine areas, even though their occurrence may be higher in zone 2 depending on the species *Chaetodipterus faber* (C.), *Citharichthys arenaceus* (E. & M.),

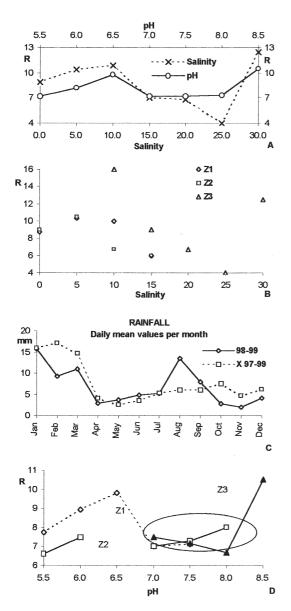


Fig. 3. – A, levels of mean species richness (mR) in all zones, according to salinity and pH at sampling time; B, levels of species richness (R) per study zone (Z1, Z2, Z3) according to the salinity; C, monthly levels of mean daily rainfall (mm) over 12 months (May 1998 to April 1999) and 27 months from June 1997 to August 1999 (X: daily mean of respective months); D, levels of mean species richness (R) per study zone (Z1, Z2, Z3) according to pH; the ellipse indicates the range of pH where species richness was the lowest, irrespective of the zone.

Eucinostomus melanopterus (B.) and *Micropogonias furnieri* (D.).

The multivariate analysis (FCA) confirms this observation with the densities for some species. It explains 100% of the 40 species distribution and densities in the three studied zones with only two axis (the zone number is reduced to three). The zones 1 and 3 are opposed (Fig. 5) on the first axis with respectively 29 and 63% of inertia contribu-

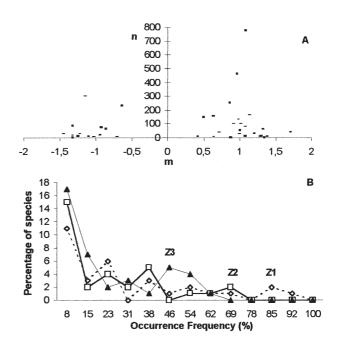


Fig. 4. – A, number (n) of individuals caught according to tide level (in metre, m) in all zones and series; negative values: ebbing tide; positive: rising tide. B, levels of species occurrence observed during the 13 series, according to the 3 zones studied. Z1: diamond; Z2: square; Z3: black triangle.

tions. The zone 2 is opposed to the previous ones on the second axis with 86% of inertia contribution. On the first axis, *B. ronchus* (12.6%), *S. rastrifer* (9,2%) and *G. genidens* (5.4%) are opposed to *P. corvaeniformis* (44.6%), *C. chrysurus* (7,2) and *C. edentulus* (3.2%) and are mainly associated with the zones 1 and 3 respectively; *E. melanopterus* (19.3%) and *E. crossostus* (9.7%) are associated with the zone 2 on the second axis.

DISCUSSION

The Bay of Guaratuba is influenced by incoming marine water all year round. Based on the geographical position of the respective influx into the Bay of continental water from the west and marine water from the east, and on the pH and salinity levels recorded from west to east in zones 1, 2 and 3, two individual areas can be identified: an upstream area under continental influence comprising zones 1 and 2, and a downstream area under marine influence corresponding to zone 3. According to the hydrological measurements of temperature, pH and salinity in all three zones, two marine seasons can be distinguished: a warm wet one in spring and summer, and a cold dry one in autumn and winter. The salinity and pH results in particular show that

Lines and columns on the axis 1 and 2 (100%)

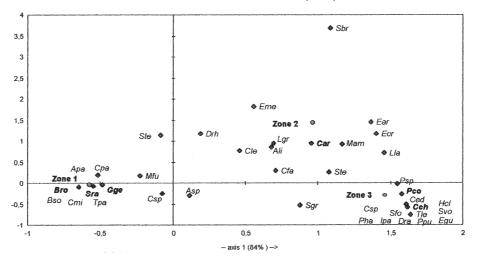


Fig. 5. – Species and zones 1, 2, 3 positions in the CFA vectorial plan 1-2; species in bold have the highest inertia contribution to the factorial axis and near their respective zone.

seasonal differences mostly affect surface water. Water at the bottom is less affected by the rains than surface water.

The effects of continental pressure are more marked in summer, when salinity and pH on the bottom are low, as is the pH at the surface. A layer of marine water, from the east end of the bay via the meeting-point with the ocean, penetrates below the upper layer of water of continental origin. The source of this water are the rivers which flow into the western edge of the bay. The layer of water at the bottom is denser and relatively less renewed by continental influxes, which explains its higher salinity and pH than that of the upper layer. Thus a large part of the water at the western edge of the bay is less renewed by water from the sea, whereas that near the mouth undergoes a much higher marine influence.

The 56 species of fish inventoried during this study are amongst those recorded for three years in the mangrove, using extra fishing equipment (the cast net), by Chaves & Corrêa (1998). Considering the development of mean species richness on the basis of these two factors in zones 1, 2 and 3, two hydrological situations can be observed, depending on continental (zones 1 and 2) or marine (zone 3) influence, separated by common temporary hydrological conditions ($10 \leq \text{salinity} \leq 15$ and $7 \leq \text{pH} \leq 8$). According to salinity, in zones 1 and 2 the mean species richness varies from 6.0 to 10.5, and in zone 3 from 4.0 to 16.0. According to pH, species richness varies from 6.6 to 9.8 in zones 1 and 2, and from 6.7 to 10.5 in zone 3. Although, irrespective of the zone or the season, there is an intermediate range of salinity and pH, as mentioned above, where species richness is relatively low, it is always higher in the marine area when compared to the continental area. This suggests that environmental factors other than immediate salinity and pH values are important for understanding the organisation and structure of the ichthyofauna. Our observations should be related to the concept of confinement in the paralic domain (Guelorget & Perthuisot 1983). Confinement in fact represents, at a given point in the ecosystem, the rate of renewal by water of marine origin. The mass of water on the system can thus be segmented according to a gradient of confinement which increases from the sea towards zones with a lower marine water renewal level. The eco-biological zonation is principally regulated by local hydrodynamics. One of the consequences of this concept is that, in the same direction, one may observe a decrease in species richness and an increase in numbers and/or biomass of the biological studied compartment. Another consequence is the phenomenon of dwarfism observed with other biological compartments is the most confined zones. In the sector under continental pressure (zone 1), most of the individuals of fish observed were of small size (Bouchereau et al. 2000a), especially when sedentary species were concerned.

In the Bay of Guaratuba, the richness of fish species decreases from the mouth towards the sectors farthest away, where renewal by marine water is the lowest, whereas numerical abundance increases. This approach and the multivariate analysis allow us to identify the presence of fish groups developing preferentially in identified confined sectors. In the most confined sector, under continental influence, most species are sedentary, like *G. genidens*, *B. ronchus* and *S. rastrifer* which are highly abundant in population. Such high concentration is explained by the fact that they complete their entire life cycle here (growth and reproduction). They form a more sedentary assemblage in

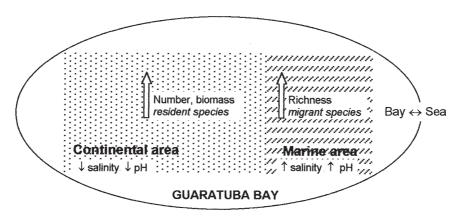


Fig. 6. – Diagrammatic representation of demographic descriptors: species richness, number and biomass, and behaviour of resident or migrant, according to the zonation observed in the Bay of Guaratuba.

the bay than do those in the marine area. In the latter sector, where marine water is more renewed (Fig. 6), the preponderant species are the migrant such as *P. corvinaeformis*, and the sporadic ones such as *Chloroscombrus chrysurus* and *Trichiurus lepturus*. The positive gradient in abundance of numbers and mass as confinement increases is confirmed by our observations. In both sectors, however, most of the 56 inventoried species present low occurrence, with sporadic and temporary species common to all.

Some of the sedentary species in the most confined sector of the bay also live in the mangrove to the north (Chaves & Bouchereau 1999). Though it is close to the meeting-point with the sea and under strong marine influence, the mangrove is probably more confined than the area defined here as "marine", implying a strong resemblance between it and the "continental" area under study here. Future hydrodynamics studies may confirm this conclusion.

In spite of zero salinity in the course of several samples, the *Rhamdia* sp catfish, a typically freshwater species, was only caught once in zone 1 in January. Nor did Chaves & Corrêa (1998) find this type of species, or other equally freshwater ones, in the mangrove sector to the north of the bay. These facts reveal the importance of the continental influence in summer in the sector the furthest from the sea. The presence of paralic and thalassic species

Confinement Concept	Observations in the Bay of Guaratuba (present study)
(Guelorget & Perthuisot 1983)	
"The organisation and structure of an assemblage in a paralic environment is more dependant of the rate of renewal in marine water than salinity. "	Although salinity and pH in a given point vary significantly during the year, spatial organisation of the fish community seem to be less dependant of the abiotic variables than the distance of this point with regard to the sea.
"The species richness in the paralic environment decreases from the less confined sector (communication with the sea) toward the most confined (inner parts). According to this gradient, the number of resident species (paralic) increases with regard to the migrant or sporadic ones (thalassic)."	The species richness is greater in the so called "marine" region than in the "continental" one. Three species found in the continental region (the most confined) make up the maximum abundance of the assemblage. There, the individuals from several population achieve their reproduction. The total abundance becomes consequently more important than in the marine region.
"Estuarian species are mainly carnivorous and omnivorous; the inferior levels of the trophic chain are just weekly exploited by fish."	The most numerous species are omnivorous with carnivorous tendency: G. genidens (Chaves & Vendel 1996), B. ronchus (Vendel & Chaves 1998), S. rastrifer (Chaves & Vendel 1998), several species of Pleuronectiform (Chaves & Serenato 1998). The piscivorous (Trichiurus lepturus (L.), Isopisthus parvipinnis (C.) - Chaves et al. 1998), and planktovorous (Clupeiform), are relatively less abundant with a limited presence in region under marine influence.

Table II. - Comparison between the theoretical confinement situation and that observed in the Bay of Guaratuba.

in these not very confined waters, where salinity is sometimes zero, shows moreover that the biological organisation of the fish population works independently of salinity (Table II).

This preliminary approach on the organisation and functioning of the populations making up the ichthyofaunal stock throughout the Bay of Guaratuba, summarised in figure 6, distinguishes two areas in this paralic ecosystem, respectively under marine and continental influence. This division is explained more by the rate of renewal in marine water than by traditional abiotic factors such as salinity and pH. The exclusive or more frequent presence of species living in the least marine zone is a feature which merits exploration. In fact, knowledge of the biological zonation of ichthyofauna in the Bay of Guaratuba should be improved by relating it to the concept of confinement established by Guelorget & Perthuisot (1983) and the hydrodynamics of the ecosystem. A deeper knowledge of the organisation and functioning of a fish assemblage living in an ecosystem belonging to the paralic domain could also allow to select fish species for fishfarming since, as pointed out by Guelorget et al. (2000), productivity and yield levels change according to the confinement degree.

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