

Seasonal and diurnal changes in the fish fauna composition of a mangrove lake in the Caeté estuary, north Brazil

by

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Abstract

Due to the construction of a road 20 years ago, the headwaters of an intertidal mangrove creek in the Rio Caeté estuary, near Bragança, Pará State (north Brazil) became a quasi-isolated lentic environment whose limnological characteristics are determined by precipitation and rare estuarine connections during high spring tides. We studied the fish fauna of this shallow artificial 0.19 km² mangrove lake. Gill net sampling conducted during 24 hour cycles in three wet and three dry season months captured 639 fish of 19 species. *Achirus achirus* (Soleidae), *Centropomus pectinatus*, *C. undecimalis* (Centropomidae), and *Mugil curema* (Mugilidae) accounted for 82 % of the total catch weight. Marine, estuarine and freshwater fish accounted for 71 %, 27 % and 2 % of the total catch weight, respectively. CPUE was low (mean: 15.8 g m⁻² 24 h⁻¹ or 0.1 individuals m⁻² 24 h⁻¹) and did not differ between seasons, but catches were highest at sunset and lowest during daylight hours. In the dry season, several species disappeared from the catches, possibly as a result of the hypersaline conditions (>40 ‰) and very low water level in the lake. The origin (fresh, brackish or marine) and size of the fish caught suggest that most species became land-locked as juveniles during the wet season (i.e. freshwater conditions (0.7 ‰), high water level) and grew up in the lake. Spawning in the lake was recorded only for *A. achirus*. Our results suggest that re-connecting the lake to the tide channels would be beneficial for those fish populations as well as for local fisheries. Road construction through mangrove areas - if not avoidable at all - should preserve the natural watershed connections to minimize habitat degradation and maintain the proper dynamics of the tides in these environments.

Keywords: Amazonia, brackish water fish fauna, coastal lacustrine waters, tropical estuary, Gonadosomatic index (GSI), habitat modification, human impacts.

Resumo

A construção de uma rodovia há 20 anos atrás transformou a cabeceira de um canal intermaré de mangue no estuário do Rio Caeté, Bragança, Pará (norte do Brasil) em um ambiente quase isolado e lêntico. As características limnológicas deste lago são determinadas por precipitação e raras conexões estuarinas durante períodos de maré de águas vivas, altas. Foi estudada a ictiofauna deste pequeno e raso lago de mangue (0.19 km²). Foram capturados 639 peixes de 19 espécies com malhadeira, durante ciclos de 24 horas em três meses do período chuvoso e em três meses no período seco. *Achirus achirus* (Soleidae),

Centropomus pectinatus, *C. undecimalis* (Centropomidae), e *Mugil curema* (Mugilidae) comporam 82 % do peso total. Peixes marinhos, estuarinos e de água doce constituíram 71 %, 27 % e 2 % do peso total, respectivamente. A CPUE foi baixa (média: 15.8 g m⁻² 24 h⁻¹ ou 0.1 indivíduos m⁻² 24 h⁻¹) e não houveram diferenças entre o período seco e o período chuvoso, mas as capturas máximas aconteceram durante o pôr do sol e as capturas mínimas durante o dia. No período seco, várias espécies desapareceram das capturas, possivelmente resultado das condições hipersalinas (>40 ‰) e nível de água muito baixo no lago. A origem (água doce, estuarino ou marinho) e o tamanho dos peixes capturados sugerem que a maioria das espécies foram retidas quando juvenis no período chuvoso (condições de água doce (0.7 ‰), alto nível de água) e cresceram no lago. Somente *A. achirus* desovou no lago. Nossos resultados sugerem que reconectar o lago para os canais intermareas seria benéfico para as populações de peixes tanto quanto para a pesca local. A construção de rodovias em áreas de mangue devem ser evitadas, porém, se necessário deveria preservar conexões naturais de drenagem para minimizar a degradação de habitats e manter a dinâmica das marés nestes ambientes.

Introduction

The coast of the north Brazilian states of Pará and Maranhão is home to the largest continuous mangrove stretch of the Americas with about 700.000 ha (LACERDA et al. 2001). The area is in a transitional stage towards the commercialization of coastal life (e.g. tourism, fisheries products etc.) as has occurred in central and south Brazilian coastal states (GLASER 2003). Part of these modifications included the construction of a ca. 40 km asphalt road in the 1970's that crosses the entire coastal mangrove plain from the hinterland at Bragança to Ajuruteua, which was formerly a fishing village at the beach and has now become a seasonal resort (Fig. 1). The road construction cut off areas from tidal water exchange and produced a large (ca. 3 km²) dieback of mangrove forest along its west side, whereas the road created a 0.19 km² mangrove lake ("lake" sensu BLABER 1997) in the center of the peninsula (Fig. 1).

The mangrove lake is regularly fished by subsistence fishermen who reported on dry season fish kills. Despite the local use, knowledge on the hydrology and the composition, dynamics and recruitment patterns of the mangrove lakes' fish fauna remained unknown. The fish fauna locked off from its tidal origin in the artificial, quasi-lentic, though unpolluted lake provides an excellent opportunity to study the effects of damming on the fish fauna composition and seasonal population dynamics in mangrove areas, thus fulfilling criteria given by WHITFIELD & ELLIOTT (2002). Understanding the ecology of the mangrove lake can provide resource users with information to predict high-risk periods and develop management options to reduce the intensity of fish kill events. Since short-term, tide-induced changes were absent in the lake, our study focused on seasonal changes in the fish fauna as well as on the nictemeral variation in the abundance of the fish species in gill net catches. The specific hypothesis of this study was that there is no difference in the ichthyofauna of the mangrove lake and the nearby mangrove.

Material and methods

Sample site

The mangrove peninsula near Bragança (Pará State, north Brazil) is located about 200 km southeast of the Amazon delta (Fig. 1). The wet season (January to June) accounts for the largest part of the 2500 mm of mean annual precipitation in the region (INMET 1992). The dry season is characterized by an arid period from September to November. The macrotide is semidiurnal with strong spring tides exceeding 4 m in tidal range.

Formerly, the lake was the afforested head of a tidal creek that drained to the east of the peninsula (A

in Fig. 1). Today, the lake (46°40'W, 00°45'S; circumference: 2.3 km) is isolated from the tide for most of the year. Its water level and hydrological characteristics are influenced only by precipitation and evaporation; nevertheless, short but significant connections occur during high equinox spring tides in March and September, via another intertidal creek of the Furo da Ostra that connects the west portion of the peninsula to the Caeté estuary (B in Fig. 1). The bottom of the lake is mud. Maximum water depth in the lake is about 2 m at the peak of the rainy season, but during the dry season the water level can decrease to <0.5 m. Secchi depth ranges between several decimeters and 1 m. There is no significant temperature, salinity or oxygen stratification. In some exceptionally dry years the lake may dry completely and fish kills occur (personal communication with fishermen).

The lake is bordered by a mixture of *Rhizophora mangle* and *Avicennia germinans* trees of about 4 m height, and during the wet season water lilies grow at the edge of the lake. To the southwest the lake adjoins to a ca. 4 km² Cyperaceae-dominated salt marsh (2 in Fig. 1) (MEHLIG 2001; REISE 2003) which is inundated for several months each year by low salinity water in the wet season.

Sample design

Gill net sampling was done monthly during a 24 h cycle in September (5+6, two 24 h cycles), October (4/5) and November 2000 (9/10) (wet season), and February (1/2), March (5/6) and April 2001 (1/2) (dry season). The nets were cleared every 3 h. We used two corridors that had been cleared of mangrove detritus before the experiment started (a and b in Fig. 1). Fifteen nylon gill nets (480 m²) were used in each corridor in ascending sequence (two nets of 20, 25, 30 and 110 mm stretched mesh size, one of 40, 50, 60, 70, 80, 90 and 100 mm mesh size; all nets 30 m long, 1 m height; except the 20 mm net that was 1.5 m high). The total gill net area was 960 m².

Predation of netted fish by swim crabs (*Callinectes* sp.) and entanglement of gill nets in the dead, broken *Rhizophora* trees distributed throughout the lake sometimes interfered with fishing.

At each sampling month, water temperature (± 0.1 °C), salinity (± 0.1 ‰; both using WTW LF197 equipped with WTW Tetracon 325 probe) and dissolved oxygen (WTW with Cellox 325 probe) were recorded at the water surface. Additionally, surface salinities in the lake and the nearby Furo da Ostra were taken almost weekly between May 2000 and June 2001. Each fish collected was identified, measured (total length, TL, to the nearest cm) and wet-weighted (Wedo balance, ± 1 g). The gonads of the most abundant species were wet-weighted (Sartorius, ± 0.01 g) and their developmental stage was assigned to four categories (immature, in maturation, mature, spawned) following VAZZOLER (1996). The gonadosomatic index (GSI) was calculated for the four most abundant species as: (Gonad wet weight \times Total wet weight⁻¹) $\times 100$. Catch per unit effort (CPUE) was calculated for biomass (g 100 m⁻² 24 h⁻¹) and abundance (individuals 100 m⁻² 24 h⁻¹) for each 3 h sampling interval.

Statistical analysis

The catches from corridor a and b were pooled though there was a trend for a higher number of species, individuals, biomass and density in corridor b than in corridor a; but the differences were not significantly different (KRUSKAL-WALLIS test). The influence of season (dry and wet) and time of day [day (09:00-15:00) (n = 19), sunset (18:00) (n = 7), night (21:00-03:00) (n = 17), sunrise (06:00) (n = 7)] on the number of species caught, number of individuals, the SHANNON-WEAVER diversity index H' (log10 on abundance), Evenness J', and the SIMPSON's Index D:

$$D = 1 / \sum_{i=1}^s P_i^2; S = \text{total species number}, P = \text{relative abundance of species } i.$$

Biomass and density was tested using the KRUSKAL-WALLIS test (SOKAL & ROHLF 1995). The length-frequency distributions of the most abundant species in the dry and in the wet season were compared using the KOLMOGOROV-SMIRNOV test (KS-test) (SOKAL & ROHLF 1995).

The similarities in species composition between months based on the number of individuals were assessed using non-metric multi-dimensional scaling (MDS) (CLARKE & WARWICK 1994). We used square root transformation to generate the BRAY-CURTIS similarity matrix. The stress of the MDS

representation - a measure of how well the ordination represents the similarities between the samples - was assessed using the classification of CLARKE & WARWICK (1994). To overcome the high variability occurring among single 3 h catches in the fish fauna composition (due to few individuals and changes in species occurrence), we pooled the catches of each 24 h cycle and analyzed the significance of seasonal differences between months only (1-way ANOSIM).

Results

Physical parameters

The annual salinity cycle in the lake was extreme when compared to the nearby Furo da Ostra tidal channel (Fig. 2). It was characterized by almost freshwater conditions during ca. seven months (February-August); then, the first September spring tide connected the lake to the tidal channel Furo da Ostra and caused an abrupt salinity rise to 11 ‰ (Fig. 2). The lake became isolated and salinity and water level were negatively correlated until the end of the dry season, when salinity reached a maximum of almost 50 ‰ in December and the lake was almost dry (water depth: 0.4 m). The first rains around Christmas rapidly re-filled the lake and salinity decreased to below 5 ‰ within one month. Later, the first February spring tide again connected the lake to the tidal channel; however, the salinity alteration was weak because the rains had already filled the lake and the Furo da Ostra had salinities similar to those in the lake. Most of year the mangrove lake was isolated and water level was mainly controlled by precipitation. Water temperature (mean: 30 °C) and dissolved oxygen content (mean: 6.5 mg l⁻¹) were usually highest in the early afternoon and lowest before sunrise.

Fish fauna

We captured 19 fish species of 15 families in the lake (Table 1). Four species accounted for 82 % of the total catch weight. The fish fauna of the mangrove lake were of relatively large sized individuals (mean TL ± SD of all fish: 23 ± 7 cm) (Table 1). The 25 mm mesh size caught 31 % of all fish, mainly *Mugil curema*, *Tarpon atlanticus* and *Centropomus undecimalis* (Table 2). The 50 mm mesh size caught 92 % of all *Achirus achirus* and 30 % of all fish. The pooled catches of gill nets with 20, 30, and 40 mm mesh size comprised 39 % of all fish caught. Smaller fish were apparently abundant, especially at the banks of the lake, but were not efficiently captured by the fishing gear used.

Marine migrant, estuarine and freshwater migrant fish accounted for 71 %, 27 % and 2 % of the total catch weight, respectively. Marine migrants dominated with 53 % of the total species number while estuarine fish accounted for 31 % and freshwater migrants for 16 %.

Of the most abundant species, three out of six species had higher TL in the wet than in the dry season indicating growth of the supposedly land-locked population (KS-test: *A. achirus*, $p < 0.001$; *C. undecimalis*, $p < 0.05$; *T. atlanticus*, $p < 0.001$) (Fig. 3). *Mugil curema* and *C. pectinatus* were significantly smaller in the wet season than in the dry season (KS-test, $p < 0.01$; $p < 0.01$) (Fig. 3). *Elops saurus* showed no seasonal changes in size.

While *M. curema* was nocturnal with highest catches at sunset in the wet season, no significant diurnal changes in the catches occurred in the dry season (Table 3). *A. achirus* was most abundant in the dry season and more active during twilight periods. *C. undecimalis* was most active at sunrise and at night in the wet season. *E. saurus* and

Astyanax sp. were most abundant in the wet season, while *Diapterus auratus* was significantly more abundant in the dry season. *Cynoscion acoupa* and *Pimelodella* sp. were only caught in the wet season while seven other species exclusively occurred in the dry season (e.g. *Pterengraulis atherinoides*; Table 1). *Epinephelus itajara* was exclusively caught at sunrise (Table 3).

Diversity index H' of the 3 h samples was generally low (Table 4). H' , evenness J' and Simpson's Index D were significantly higher in the wet than in the dry season (Table 4). J' was lowest at sunrise and highest at daytime while H' and D did not show any diel pattern. Number of individuals, density, catch weight and biomass did not differ between seasons, but were always highest at sunrise and lowest at daytime (Table 4). The number of species did not differ between seasons or time of day but on a monthly basis it was highest in September (17 species) and low in all other months (7-9 species). Except for *C. pectinatus* and *Astyanax* sp., which recurred in the wet season, seven species were not caught again after the dry season salinity increase in September (Table 1). The average density and biomass (\pm SD) in the mangrove lake was 0.10 fish m^{-2} 24 h^{-1} (\pm 0.1) and 15.8 g m^{-2} 24 h^{-1} (\pm 15.3).

GSI of *A. achirus* peaked in April (3.6 ± 0.1 ; $n = 48$) suggesting reproductive activity in the lake in the wet season. The GSI values for *M. curema* ($n = 49$), *C. pectinatus* ($n = 23$) and *C. undecimalis* ($n = 55$) were on average <0.1 and showed no seasonal change.

The MDS separated dry season samples (on the left) from those of the wet season (on the right) (Fig. 4). Despite a low stress value of the MDS (0.01), the compositional changes between dry and wet season were not significantly different (1-way ANOSIM, $p = 0.057$).

Discussion

The null hypothesis that there are no differences in the ichthyofauna between the mangrove lake and the nearby mangrove area could be rejected. Compared to adjacent natural intertidal mangrove creeks that hold more than 50 fish species (BARLETTA et al. 2003; KRUMME et al. 2004), species richness in the lake is low. This seems to be primarily related to the extreme variability in the environmental conditions (salinity, water level) and the small size of the lake. Other factors that could explain the low species number are: relatively recent formation of the lake, isolation for most of the year, shallow bathymetry, and a possibly low selectivity of the fishing method employed in the present study.

12 and 13 of the 19 species registered in the lake also occurred as juveniles in nearby tidal creeks surveyed by BARLETTA et al. (2003) and KRUMME et al. (2004), respectively. The presence of *Astyanax* sp. and *Rhambella* sp., two generalist species of freshwater origin, emphasized the extreme conditions characterizing the mangrove lake environment. Interestingly, this is the first record for the Caeté estuary of *C. undecimalis* and *C. pectinatus* that apparently prefer low salinity conditions and shallow waters (FRASER 1978; PETERSON & GILMORE 1991; ALIAUME et al. 1997), and of *E. saurus* whose juveniles are common in lagoons and hypersaline bays (CERVIGÓN et al. 1992).

It is striking that several other abundant intertidal mangrove fish species (see KRUMME et al. 2004) were completely absent from the lake. We do not know what exactly caused this situation; whether these species are unable to resist the variable

environmental conditions in the lake, suffer from heavy predation or strongly rely on intertidal rather than lentic food resources. If the latter holds true, then these species should be considered obligate intertidal fish species whose populations depend on mangrove resources and tidal dynamics.

The fish fauna of coastal lakes is usually derived from the sea (BLABER 1997), which was also the case in the present study. The juveniles of many of the marine species occurring in the lake are known to use brackish shallow waters as nurseries during their juvenile stage (e.g. CERVIGÓN et al. 1992; BARLETTA-BERGAN et al. 2002).

Strong spring tides are related to the immigration of large numbers of fish into the intertidal mangrove zone (KRUMME 2004; KRUMME et al. 2004). Probably most species colonize the lake accidentally during the connection provided by high spring tides. Due to the lack of a strong ebb tide trigger in the lake and due to a supposed difficulty to find the inflow creek, the fish become land-locked for most of year and grow up there. Thus, each tidal connection would lead to the colonization of the lake by a random subset of estuarine fish. The subsequent differential mortality of several immigrant species shapes the lake's fish assemblage.

The intertidal migration of mangrove fish is significantly stronger during nocturnal tides (KRUMME 2004; KRUMME et al. 2004). It is therefore not surprising that the most abundant species in the lake were most active during twilight hours or at night. Furthermore, many species were predatory fish that benefit of the twilight hours to catch their prey (e.g. HELFMAN 1993).

While most species were recorded in September, diversity was highest in February. The lower dry season values of diversity, evenness and Simpson's index can be mainly attributed to the dominance of *A. achirus*. In the dry season the low water level in the lake may have increased the gill net efficiency towards demersal flatfish since a large portion of the nets were set very close to the substrate.

The tidal connection in September launched the dry season salinity increase to hypersaline levels and therefore created unfavorable conditions for most of the fish fauna in the lake. Despite their euryhalinity, several species seemed to have died off, apparently a common phenomenon in the lake as confirmed by local fishermen. In contrast, the change in environmental conditions resulting from the wet season tidal connection in February seemed to be less severe because both the lake and the adjacent estuarine waters were almost freshwater due to the strong rains in that period of the year. It is therefore likely that fish immigration to the lake mainly occurs during estuarine connections in the wet season due to more similar salinities and physical connectedness. This may also be the period when emigration of larger fish from the lake to the estuary takes place.

Some species survived the hypersaline period in the lake as indicated by the presence of significantly larger specimens in the wet than in the dry season. Land-locked growth in the lake is also indicated by larger average sizes in those fish species that occur both in the lake and in the adjacent mangrove creeks. The reason why two species were significantly smaller in the wet season is unclear but this should not necessarily be linked to emigration of larger individuals or to immigration of smaller ones from the estuary. The small sample size, a reduction of larger-sized fish by artisanal fishing, or changes in diurnal activity patterns and hence, effectiveness of the gill net sampling in the wet season may represent alternative explanations.

We know very little about the ecophysiology of most of these tropical fish species, but the robustness of some species such as *A. achirus* or *C. undecimalis*, to survive under the variable conditions of the lake environment may indicate their attractiveness for aquaculture (PAIVA ROCHA & OKADA 1980). *A. achirus* was the only abundant species that apparently could maintain its population by successfully reproducing in the lake. It exhibited a reproductive pattern similar to conspecifics outside in the Caeté bay where larvae abundances peaked in March (BARLETTA-BERGAN et al. 2002).

The CPUE in terms of abundance ($0.1 \text{ fish m}^{-2} 24 \text{ h}^{-1}$) was similar to freshwater systems like the Rio Mucajá ($0.62 \text{ fish m}^{-2} 24 \text{ h}^{-1}$; FERREIRA et al. 1988) and some clear or blackwater rivers in Rondônia ($0.07 \text{ fish m}^{-2} 24 \text{ h}^{-1}$; SANTOS 1991). A comparison of the CPUE in terms of biomass ($15.8 \text{ g m}^{-2} 24 \text{ h}^{-1}$) with Amazonian floodplain environments revealed values lower than blackwater areas ($41 \text{ g m}^{-2} 24 \text{ h}^{-1}$; SANTOS 1991) and substantially lower values than whitewater floodplain areas near Manaus ($190 \text{ g m}^{-2} 24 \text{ h}^{-1}$; SAINT-PAUL et al. 2000) and the Rio Trombetas ($128 \text{ g m}^{-2} 24 \text{ h}^{-1}$; FERREIRA 1993). Despite its estuarine origin, the lake productivity seems to be relatively low, probably due to the extreme salinity regime and the month-long isolation from tidally supplied nutrients. We have no information about the growth performance and ages at capture of the fish and it is therefore difficult to ultimately estimate the long-term productivity of the mangrove lake. The average fish biomass data of nearby intertidal mangrove creeks [0.11 fish m^{-2} and 2.1 g m^{-2} (BARLETTA et al. 2003); 0.2 fish m^{-3} and 1.4 g m^{-2} (KRUMME et al. 2004)] resulted from block net sampling at slack high water and thus, are not readily comparable to our estimates.

Unfortunately, we found no ichthyofaunal studies from mangrove areas transformed into lakes that could be compared with our study area. A comparison with black and whitewater environments with similar annual pulses was also of limited relevance due to salinity and species assemblage differences.

Abandoned shrimps ponds would provide a suitable comparison because they are mostly constructed in former mangrove areas and resemble lakes when levees are in place. However, these areas are polluted and studies concerning recovery are rare. To the best of our knowledge, the present study is the first to address the effects of damming on fish assemblages in mangrove areas.

The results suggest that the lake should be re-connected to the mangrove system through the tidal creek 1 (Fig.1). The substitution of a road stretch by a bridge would partially drain the lake, allowing for free exchange of tidal water and fish, ensuring a natural recovery of the area. Another possibility would be to deepen the tidal creek 2, yet the topography makes this logistically difficult. If no rehabilitation measures were taken, one could recommend harvesting of fish before each September equinox by local fishermen to prevent fish kills in the late dry season and use the fish biomass that has grown up during the wet season period.

In intertidal areas, road construction that does not consider the course of the watersheds can obstruct the flow of the tides, and large areas can become cut off from the regular supply of tidal water, nutrients and nekton. Depending on the local topography, road blockage of tidal influx can result in either dry plateau areas, or flooded depressions or lakes. These newly formed lentic aquatic habitats emerge in an environment formerly characterized by the daily tidal oscillation, and thus may affect the habitat structure and dynamics of fish populations. Similarly, in 1975 the 324 ha Jansen Lagoon in São Luis, Maranhão, north Brazil, was formed due to the construction of a road to

connect two city districts, which obstructed the channel connecting the former mangrove area to the Atlantic coast. Today the Jansen Lagoon located near downtown São Luis is highly polluted (e.g. HERENIO & COSTA 2003). Similar losses of mangrove areas are likely to occur if coastal development continues without regard to the processes that control mangrove ecosystems, notably the tidal water exchange.

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Table 1: Fish species caught with gill nets in a mangrove lake, Caeité estuary, near Bragança (Pará State, north Brazil) between September 2000 and April 2001. MC: Migratory category according to BARLETTA (1999) and KRUMME et al. (2004); M: Marine migrants, E: Estuarine fish, F: Freshwater migrants. n: Total abundance. %: Percent of occurrence in n = 54 samples. Monthly catch per unit effort values are provided in g 100 m⁻² 24 h⁻¹. Mean total length (cm ± SD) and the minimum and maximum fish size is given.

Species	MC	n	%	Dry season				Wet season				TL
				Sep	Oct	Nov	Feb	Mar	Apr	CPUE	CPUE	
1 <i>Achirus achirus</i> (Soleidae)	E	206	56	2.27	2.56	0.25	0.69	0.13	0.19	18 ± 2; 11-28		
2 <i>Mugil curema</i> (Mugilidae)	M	104	61	0.41	0.13	0.38	1.25	2.25	0.88	23 ± 5; 14-44		
3 <i>Centropomus undecimalis</i> (Centropomidae)	M	87	50	0.19	0.13	1.69	0.88	1.13	0.88	29 ± 6; 17-51		
4 <i>Tarpon atlanticus</i> (Megalopidae)	M	69	35	0.66	0.06	0.06	0.44	1.13	0.06	32 ± 6; 24-49		
5 <i>Centropomus pectinatus</i> (Centropomidae)	M	32	26	0.39			0.19	0.25		24 ± 4; 16-31		
6 <i>Elops saurus</i> (Elopidae)	M	29	30		0.25	0.06	1.06	0.13	0.31	34 ± 3; 28-38		
7 <i>Pterengraulis atherinoides</i> (Engraulidae)	E	26	28	0.13	0.31	0.81				17 ± 2; 14-20		
8 <i>Diapterus auratus</i> (Gerreidae)	M	24	26	0.19	0.56	0.06	0.06	0.06		15 ± 1; 12-17		
9 <i>Rhamdella</i> sp. (Pimelodidae)	F	22	17	0.03		0.13	0.06		0.94	18 ± 3; 14-23		
10 <i>Astyanax</i> sp. (Characidae)	F	11	17	0.02			0.13	0.31	0.19	12 ± 1; 11-14		
11 <i>Cynoscion acoupa</i> (Sciaenidae)	M	9	11						0.56	17 ± 2; 13-21		
12 <i>Epinephelus itajara</i> (Serranidae)	M	5	7	0.06				0.06		24 ± 5; 18-32		
13 <i>Lutjanus jocu</i> (Lutjanidae)	M	4	7	0.05		0.06				17 ± 1; 15-18		
14 <i>Anchovia clupeioides</i> (Engraulidae)	E	2	4	0.03						15-16		
15 <i>Colomesus psittacus</i> (Tetraodontidae)	E	2	4	0.03						21-24		
16 <i>Lycengraulis grossidens</i> (Engraulidae)	F	2	4	0.03						14-15		

17 <i>Oligopites saurus</i> (Carangidae)	M	2	4	0.02	0.06		18-24			
18 <i>Pimelodella</i> sp. (Pimelodidae)	F	2	4			0.13	12-13			
19 <i>Symphurus</i> sp. (Cynglossidae)	E	1	2	0.02			13			
TOTAL		639		4.50	4.00	3.50	4.75	5.44	4.12	23 ± 7

Table 2: Fishing efficiency of the different mesh sizes employed in a mangrove lake, north Brazil. Names are given for those species that were caught with n > 20 individuals in a net. **A. achirus* accounted for 92 % of the 189 fish caught.

Mesh size (mm)	No. of fish	Species
25	196	<i>M. curema</i> , <i>T. atlanticus</i> , <i>C. undecimalis</i>
50	189	<i>A. achirus</i> *
30	114	<i>C. undecimalis</i>
20	91	<i>M. curema</i>
40	40	
70	4	
60	3	

Table 3: Species with significant differences (KRUSKAL-WALLIS test) in their total catch weight by season (D: Dry season 2000; W: Wet season 2001) and through a full diel cycle (SS: Sunset; N: Night; SR: Sunrise; D: Daytime) in a mangrove lake, Caeté estuary, near Bragança (Pará, Brazil). n = 54 gill net samples. Significance levels: *p < 0.05; **p < 0.01; ***p < 0.001.

Species	Season	Time of day
<i>M. curema</i>		*** (SS > N > SR > D) (wet); n.s. (dry)
<i>A. achirus</i>	* (D > W)	** (SR > SS > N > D) (dry); n.s. (wet)
<i>C. undecimalis</i>		* (SR > N > SS > D) (wet); n.s. (dry)
<i>E. saurus</i>	*** (W > D)	
<i>D. auratus</i>	** (D > W)	
<i>Astyanax</i> sp.	** (W > D)	
<i>E. itajara</i>		* (SR > D; SS, N: 0) (dry); SR only (wet)

Table 4: KRUSKAL-WALLIS test results of the influence of season (D: dry season 2000; W: Wet season 2001) and time of day [D: Daytime (n = 20); SS: Sunset (n = 7); N: Night (n = 20); SR: Sunrise (n = 7)] on eight response variables of the fish fauna caught with gill nets (960 m²) in a mangrove lake, Caeté estuary, near Bragança (Pará, Brazil). Significance levels: *p <0.05; **p <0.01; ***p <0.001. Time of day was tested separately for each season. Significant differences for a variable always occurred in both seasons, therefore the lowest significance of a season and overall averages are given.

Variable	Season	Time of day
J'	** (W > D; 0.93 > 0.81)	* (D > SS > N > SR; 0.95 > 0.88 > 0.83 > 0.76)
H'	* (W > D; 0.52 > 0.38)	
Simpson's D	** (W > D; 3.18 > 2.37)	
Number of individuals		* (SR > SS > N > D; 23 > 14 > 12 > 5)
Density (Ind. 100 m ⁻² h ⁻¹)		* (SR > SS > N > D; 0.78 > 0.47 > 0.43 > 0.17)
Catch weight (g)		* (SR > SS > N > D; 3814 > 2235 > 1847 > 887)
Biomass (g m ⁻² h ⁻¹)		* (SR > SS > N > D; 1.32 > 0.78 > 0.64 > 0.31)
Number of species		SR > N = SS > D; 6 > 4 = 4 > 3

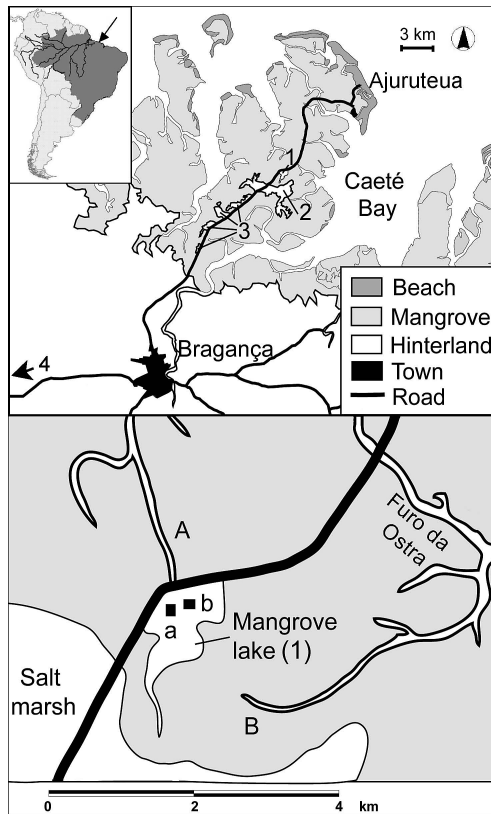


Fig. 1:

Gill net sampling corridors a and b in the mangrove lake (1) in the middle Caeté estuary, north Brazil. 2: Salt marsh; 3: Mangrove dieback area at the west of the road; 4: Meteorological station at Tracuateua. A: Former tidal connection draining to the west of the peninsula; B: Temporary connection at high spring tides via Furo da Ostra draining to the east of the peninsula. The road PA-253 connects Bragança with the fishing village Ajuruteua at the Atlantic coast.

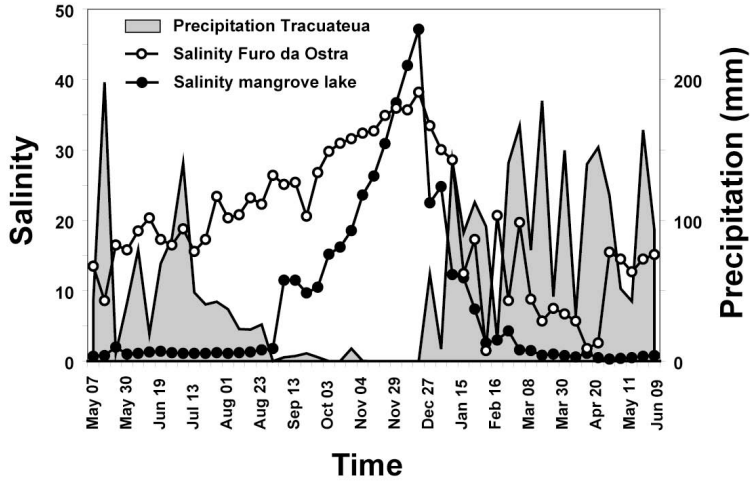


Fig. 2: Quasi-weekly surface salinity measurements in the mangrove lake and the nearby tidal mangrove channel Furo da Ostra, and precipitation at Tracuateua (nearest permanent weather station (INMET): 01°05'S, 47°10'W) between May 2000 and June 2001.

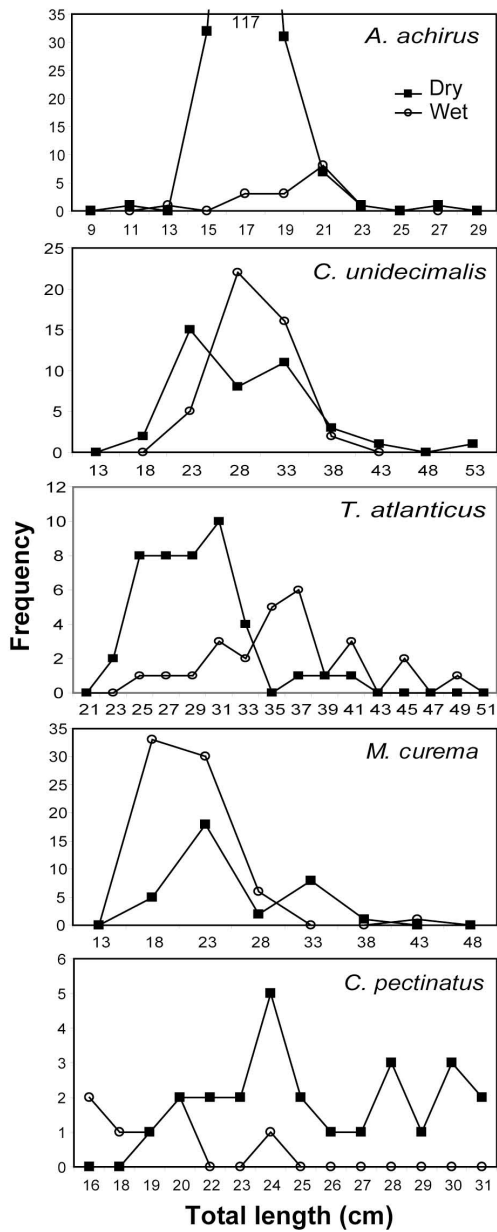


Fig. 3: Length-frequency distributions of the top five fish species in the mangrove lake, Caeté estuary, north Brazil, in the dry season 2000 (filled squares) and in the wet season 2001 (open circles).

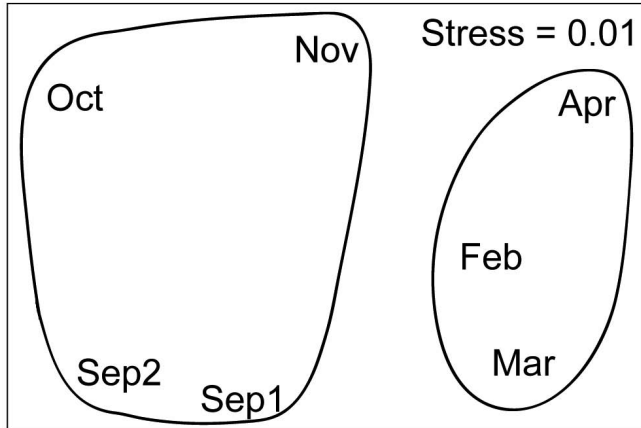


Fig. 4:

Multidimensional scaling (MDS) plot of seven 24 h gill net samples taken in three dry season months (September, October, November 2000) and three wet season months (February, March, April 2001) in the mangrove lake, Caeté estuary, north Brazil. Similarities refer to the abundance per species. In September, two 24 h cycles were sampled.

