Aquatic Living Resources

Tidal and diel changes in the structure of a nekton assemblage in small intertidal mangrove creeks in northern Brazil

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Abstract – Changes in nekton community structure in north Brazilian intertidal mangrove creeks were studied by setting block nets at high water in the wet season 1999. From a total of 47 species (27 families), the most abundant were: *Cathorops* sp. (Ariidae), *Colomesus psittacus* (Tetraodontidae), *Hexanematichthys herzbergii* (Ariidae), *Pseudauchenipterus* nodosus (Auchenipteridae), the shrimp *Fenneropenaeus subtilis* (Penaeidae), *Anchovia clupeoides* (Engraulidae), *Mugil* spp. (Mugilidae), and *Anableps anableps* (Anablepidae). Diversity H' was low (0.9). Mean values of fish density and biomass ($\pm$ S.E.) were 0.2 ± 0.1 fish m^{-3} and 2.6 ± 0.7 g m^{-3} or 1.4 ± 0.4 g m^{-2}, respectively. The high proportion of juvenile fish (87%) and shrimps point to the importance of intertidal mangrove creeks for fish nurseries. The number of species was highest at spring tide-night and lowest at neap tide-day. Evenness J' was lowest at spring tide-night when more rare species entered and dominant species increased in quantitative proportions. Four different species assemblages were identified as being triggered by factor combinations such as "tide" and "time of day": spring tide-night, spring tide-day, neap tide-night and neap tide-day. High-water level influenced the species assemblages, but salinity and water temperature did not. Abundance of 14 species correlated positively with the high-water level. Strong spring tides yielded extraordinary high nekton catches, suggesting that high-water level is an important parameter in the tidal migration of fish. Most fish entered the mangrove to feed. Predation pressure was considered to be low because of the presence of only a few, mainly juvenile predators. Beach seining in the subtidal parts at low water revealed a high biomass (30 ± 14 g m^{-2}). Larger fish withdraw to depressions, small fish and juvenile shrimp were abundant near the shallow banks, suggesting inter- and intraspecific splitting of the migration routes when returning from the intertidal zone at ebb tide. To cover the entire short-term range of tidal ichthyofauna responses, a sample design should consider the spring/neap and the day/night cycle.

Key words: Water level / Nursery / Migration / Community structure / Tropical Fish / Shrimp / Beach seine / Amazon

Résumé – Variations nycthémérales et en fonction de la marée de la structure de l'assemblage du necton dans des criques de la mangrove, nord du Brésil. Des changements de la structure du necton des criques de la mangrove, en zone intertidale, nord du Brésil, ont éte étudiés, en fermant celles-ci au moyen de filets, à marée haute et lors de la saison humide en 1999. Des 47 espèces (27 familles), les plus abondantes sont : *Cathorops* sp. (Ariidae), *Colomesus psittacus* (Tetraodontidae), *Hexanematichthys herzbergii* (Ariidae), *Pseudauchenipterus nodosus* (Auchenipteridae), la crevette *Fenneropenaeus subtilis* (Penaeidae), *Anchovia clupeoides* (Engraulidae), *Mugil* spp. (Mugilidae), et *Anableps anableps* (Anablepidae). L'indice de diversité H' est faible (0,9). Les valeurs moyennes de densité et de biomasse des poissons ($\pm$ S.E.) sont $0,2 \pm 0,1$ poisson m^{-3} et $2,6 \pm 0,7$ g m^{-3} ou $1,4 \pm 0,4$ g m^{-2}, respectivement. La forte proportion de poissons juvéniles (87 %) et de crevettes montre l'importance de ces criques comme nourriceries. Le nombre d'espèce est le plus élevé lors de marées nocturnes de vives-eaux, et le plus faible dans la journée à marées de mortes-eaux. L'indice de régularité J' est le plus faible à marées nocturnes de vives-eaux lorsque davantage d'espèces « rares » entrent et les espèces dominantes augmentent en proportion. Quatre assemblages d'espèces différents sont identifiés comme étant caractéristiques, par combinaison de facteurs tels que le coefficient de marée et l'heure (jour/nuit). Le niveau de l'eau influence l'assemblage des espèces mais non la salinité et la température de l'eau. L'abondance de 14 espèces sont corrélées positivement avec des niveaux d'eau élevés. De fortes marées de vives-eaux produisent des captures importantes, ce qui laisse supposer que le niveau d'eau est un paramètre important dans la migration des poissons liée à la marée. La plupart des poissons entre dans la mangrove pour se nourrir. La pression de prédation est considérée comme faible car peu de prédateurs, mais principalement des juvéniles, sont présents. Les pêches à la senne de plage, en zones subtidales, à marée basse montrent une forte biomasse (30 ± 14 g m^{-2}). Les gros poissons se réfugient dans les dépressions, tandis que les petits et les crevettes juvéniles sont abondants à faible profondeur près de berges ; ainsi, à marée descendante, les routes inter- et intraspécifique de migration se sépareraient. Afin de couvrir la période entière des réponses à court terme de l'ichtyofaune en fonction de la marée, un plan d'échantilllonnage devrait considérer les marées de vives-eaux/mortes-eaux et les cycles jours/nuits.

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1 Introduction

Mangroves are considered important fish nurseries (Robertson and Duke 1987; Davis 1988; Robertson and Duke 1990; Sasekumar et al. 1992; Laegdsgaard and Johnson 1995; Laroche et al. 1997; Nagelkerken et al. 2000) because they provide advantageous conditions for growth in a protected habitat (Laegdsgaard and Johnson 2001).

The northeast coast of South America is home to the second largest continuous mangrove ecosystem of the world (Kjerfve and de Lacerda 1993). In spite of the extent of this vast mangrove ecosystem, few studies have dealt with its fish fauna so far (e.g. Boujard et al. 1988; Tito de Morais and Tito de Morais 1994; Batista and Rêgo 1996; Castro 2001; Barletta-Bergan et al. 2002a,b; Barletta et al. 2003). These studies basically focus on longer-term variations related to seasonal salinity fluctuations. The coast near the mouth of the Amazon River is characterized by semidiurnal macrotides that may intensively influence short- and medium-term variations in mangrove fish communities. Based on the studies of Barletta et al. (2003) and Barletta-Bergan et al. (2002a,b) in the mangrove estuary of the Caeté River near Bragança (Pará, north Brazil), the present study investigates temporal changes in mangrove fish assemblages related to the neap/spring tide alternation and the day/night cycle.

In other mangrove areas, changes in the fish fauna according to the lunar periodicity (Davis 1988; Laroche et al. 1997) and the spring/neap tide alternation have been shown (Blaber et al. 1995; Laroche et al. 1997; Wilson and Sheaves 2001). Various authors have reported on diel activity changes (Helfman 1993; Blaber et al. 1995; Lin and Shao 1999). While lunar and diel cycles determine intertidal properties, a clear quantifying evidence of influencing migration patterns of juvenile fish is still lacking.

Movements over short temporal and spatial scales are most likely coupled tightly with habitat and resource usage (Morrison et al. 2002). As many fish species are only temporary residents of the mangrove, investigations with a higher temporal resolution of habitat use are necessary to understand the importance of the mangrove for the fish.

Robertson and Blaber (1992) assumed that fish reside in the main channels at low water (LW) from where they immigrate again into the mangrove forest at flood tide. However, the habitat utilization of juvenile fish in the subtidal mangrove parts at LW is essentially unknown (Laegdsgaard and Johnson 1995) although intertidal fish become physically concentrated in these areas each low tide.

Therefore, this paper focuses on temporal patterns in the community structure of mangrove ichthyofauna to understand tidal-induced fish migration between the subtidal parts of an estuary and its intertidal tributaries.

2 Study area and sample site

The Caeté estuary is located about 200 km southeast of the Amazon delta (Fig. 1). The peninsula (about 220 km^2) on the western side of the Caeté River is presently under study by the interdisciplinary German-Brazilian MADAM project (Mangrove Dynamics and Management) (Berger et al. 1999).
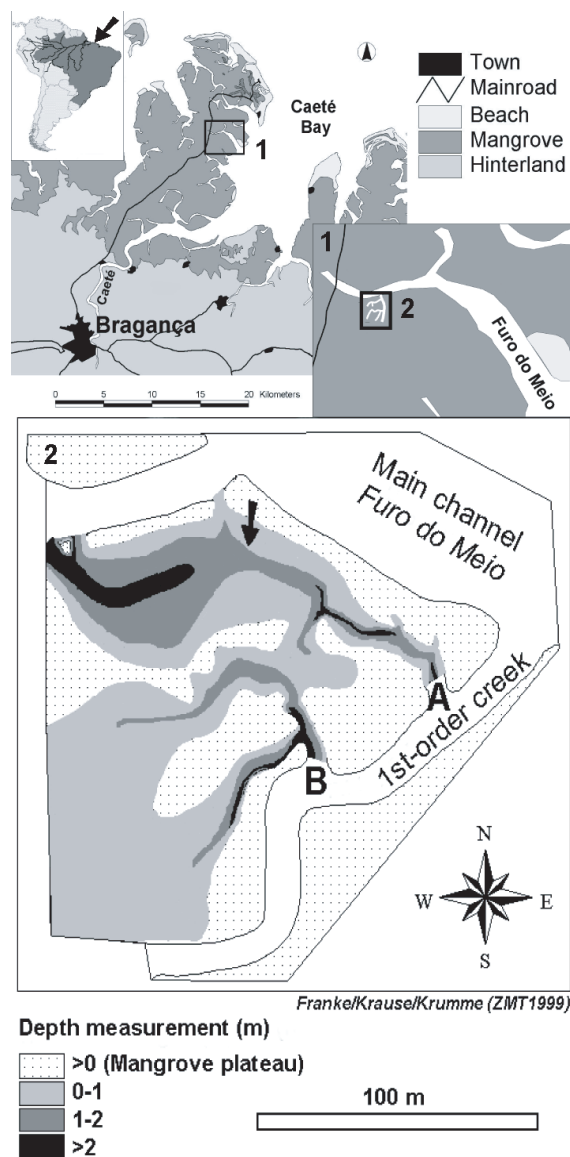

Fig. 1. Mangrove peninsula southeast of the Amazon estuary, north Brazil. The location of the Furo do Meio channel in the center of the mangrove peninsula near the city of Bragança, and the study site, in the upper reaches of the Furo do Meio. The creek entrances of the two 2nd order intertidal creeks labeled A and B were blocked at high water. The arrow in the upper reaches of creek A indicates a strong flattening acting as a natural topographical barrier during neap tides, limiting water exchange towards the adjacent creek system.

A detailed description of the study area can be found in Krause et al. (2001). No seagrass beds or coral reefs exist in vicinity of the Caeté estuary.

The wet season (January to June) accounts for the largest part of the 2500 mm of mean annual precipitation in the region (INMET 1992). Salinity can fall below 5 and exceed 35 in the wet and dry season, respectively. Wet season Secchi depth is on average 20 ± 1 cm S.E. at neaps and 12 ± 1 cm at springs. The tide is semidiurnal with a mean tidal range of 2.5 m at neaps and 4.0 m at springs. The tide is asymmetric, flood and ebb tide lasting ca. 4 and 8 hours, respectively.

Table 1. Sample design and physical parameters of 17 high-water block net samples (*tapagem*) in intertidal mangrove creeks, north Brazil, in the wet season 1999. Tide: S (Spring tide), N (Neap tide); Time of day (time): D (Daytime), N (Night); Creek: A (creek A), B (creek B); +: Positive impact of wind on maximum water depth at high water (HW). Temp: Water temperature.

| No. | Date | Lunar phase | Treatment factors | | | Max. Depth at HW (m) | Wind | Time of HW | Salinity (psu) | Temp. (°C) |
			Tide	Time	Creek					
1	Feb. 8	☽ Wane	N	D	B	1.46		11:00	27.8	27.5
2	Feb. 9	☽ Wane	N	N	A	1.19		23:25	28.8	28.8
3	Feb. 15	● New moon	S	N	B	2.64	+	18:35	30.4	29.5
4	Feb. 16	● New moon	S	D	A	2.39		07:10	29.9	28.4
5	Feb. 22	☾ Wax	N	D	A	2.12	+	10:45	27.3	28.2
6	Feb. 22/23	☾ Wax	N	N	B	1.89		23:00	27.8	28.2
7	Mar. 2	○ Full moon	S	N	B	2.82		19:10	18.5	27.8
8	Mar. 3	○ Full moon	S	D	A	2.51		07:35	17.9	27.0
9	Mar. 10	☽ Wane	N	D	A	1.36		11:55	16.4	28.4
10	Mar. 11	☽ Wane	N	N	B	1.12		00:55	16.4	28.6
11	Mar. 17	● New moon	S	N	A	3.11		18:55	10.7	28.2
12	Mar. 18	● New moon	S	D	B	2.89		07:25	10.2	27.6
13	Mar. 24	☾ Wax	N	D	B	2.01	+	11:20	8.1	27.5
14	Mar. 24/25	☾ Wax	N	N	A	1.56		23:35	8.1	27.0
15	Mar. 31	○ Full moon	S	N	A	2.64		18:30	9.6	28.0
16	Apr. 1	○ Full moon	S	D	B	2.54		06:50	10.2	27.4
17	Apr. 1	○ Full moon	S	N	B	2.57		19:10	10.2	27.9

About 110 km^2 of the peninsula are covered by mangrove, of which parts are connected to the estuary by tidal channels, e.g. the 4.5 km long and dead-ending "Furo do Meio" (Fig. 1). The mangrove forest proper is only inundated fortnightly at spring tides ("plateau mangrove"). In the funnel-shaped network of shallow tidal creeks, wind can influence tidal height in the range of decimeters.

The two selected tidal creeks A and B (00°87′40″ S, 46°64′50″ W) are 2nd order creeks located in the muddy upper reaches of the Furo do Meio (Fig. 1). They are ca. 70 m long and completely covered by mangrove canopy. The mouths of the creeks are approximately 8 m wide; the creek bed was 2 m deep and rose gradually while progressing into the forest. The mouths of the creeks were approximately 1.1 m above the mean low water level and therefore, only inundated for ca. 6 h 30 min each tidal cycle (Fig. 1). The sample site was dominated by *Rhizophora mangle* and single stands of *Avicennia germinans* on elevated sites and thus is representative for large parts of the mangrove on the peninsula.

3 Materials and methods

We blocked the mouth of two intertidal mangrove creeks at slack high water (HW) with a 10×3 m nylon net (12 mm stretched mesh size). The nekton fauna was collected during ebb tide. Between February and April 1999, sixteen samples were taken eight times a month, to take account of the four different combinations of tide or lunar phase and daylight conditions: spring tide-night, spring tide-day, neap tide-night and neap tide-day (for the remainder of this paper we denote the factor combinations as SN, SD, NN and ND, respectively) (Table 1). Due to the lunar postponement of ca. 6 hours, HW at spring tide occurred after dusk (19:00) and dawn (7:00) (SN, SD) whereas HW at neap tide occurred at approximately midnight (1:00) and midday (13:00) (NN, ND) (Table 1).

Sample No. 17 (SN) repeated No. 16 (SD) in creek B (Table 1). Although $n = 1$, we use this experiment to provide preliminary evidence of day/night differences, the effect of substrate disturbance on species immigration, and preference of a certain creek from tide to tide. Species with $n > 5$ specimens were compared using the Chi square test.

Catches were transported on ice to the laboratory, measured (total length (TL) in cm below), weighed (Sartorius LC 4200 S; ±0.01 g) and identified to the lowest taxonomic level possible (FAO species identification sheets 1977; Cervigón 1991, 1993, 1994, 1996; Cervigón et al. 1993; Smith 1997). Apparently four mullet species were subsumed as *Mugil* spp. We use *Cathorops* sp. (Ariidae) for what is locally called "Uricica branca" and determined as *C. pleurops* in Barletta et al. (2003). Apparently, *C. spixii* is a species complex, probably with different valid species along its distribution in Central and South America (Higuichi, Museu Paraense Emílio Goeldi, pers. comm. in Camargo and Isaac 1998).

Stomach fullness of *Cathorops* sp., *Hexanematichthys herzbergii*, and *Pseudauchenipterus nodosus* was determined visually and assigned to one of five fullness categories: 0, 0−25, 25−50, 50−75, 75−100%. We tested for differences between SN, SD, NN and ND using the Kruskal-Wallis test and the Nemenyi test for post-hoc analysis.

For each sampling event, water temperature (±0.1 °C), salinity (±0.1; both using WTW LF197 equipped with WTW Tetracon 325 sonde) and tidal height (±1 cm) were recorded at the mouth of the creeks at HW.

Since HW level varied each tide, catch weights and abundance were standardized to biomass ($g\,m^{-3}$ or $g\,m^{-2}$) and density (number of fish m^{-3} or number of fish m^{-2}). The sample site was surveyed and relationships between HW level and the volume of water and the area inundated were established for each creek.

The fish species caught were assigned to three migratory categories following Day et al. (1981), Blaber (1997), Barletta (1999); and to six feeding categories following Longhurst and Pauly (1987) and own observations, based on qualitative analysis of the diet composition of the species collected. The stomachs of fish larger than ca. 5 cm TL were opened and a qualitative list of the diet for each species was made. In piscivorous species, the number of prey items was counted.

We used TL from the literature and our own observations to determine the proportion of juveniles and adults in the catches. Adults of *Anableps anableps*, *Cathorops* sp. and *Stellifer naso* were sexed and TL at which half of the population contained mature gonads (L_{50}) was established graphically (±0.1 cm). For the shrimp *Palaemon northropi* the TL was determined when 50% of the individuals caught were egg-carrying females. Sex-specific occurrence of *Cathorops* sp. was tested by a $R \times C$ test of independence using the G-test. Post-hoc analysis was only applied for male *Cathorops* sp. recognizable as mouth-breeding specimens (unplanned test of the homogeneity of replicates tested for goodness of fit) (Sokal and Rohlf 1995).

The influence of SN, SD, NN and ND on the number of species, the Shannon-Weaver diversity H', as log 10 based on abundance and Evenness J' was tested using the Kruskal-Wallis test. Species abundance was correlated with salinity to identify seasonal migration trends. Abundance, biomass and total catch weight were analyzed using 2-way and 3-way analysis of variance (ANOVA). Only species with $n > 10$ individuals were considered for analysis.

The similarities in species composition between the samples were assessed using non-parametric multi-dimensional scaling (MDS) (Primer 5; Clarke and 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 and Warwick (1994). Significance of differences between samples was tested using the analysis of similarities (ANOSIM) for a 2-way crossed case with the treatment factors "tide" and "time of day". Circles scaled in size to represent the values of abiotic parameters (HW level, salinity and water temperature) were superimposed onto the faunistic 2-dimensional MDS configuration to visualize obvious concordance between arrangement of samples and changes in abiotic parameters.

To study the structure of the nekton assemblage in the subtidal parts of the mangrove at LW, we conducted 16 scientific beach seine catches at neap tide in the main channel (the same net used for block netting) at both daytime and night in August 2002 during the early dry season (salinity: 26.8 psu). Two people dragged and hauled the net straight to the shore, covering areas between ca. 25 and 65 m^{-2} of the shallow channel bank for each haul (maximum depth ca. 1.7 m). Additionally, we analyzed artisanal catches taken with a gillnet at daytime-LW in October (salinity: 31.1 psu) at spring and neap tide in the dry season 2000 (50 × 3 m, 60 mm stretched mesh size; maximum depth ca. 3 m). Three fishermen enclosed an area with the net; one beat the water surface with a large branch while the others dived to startle the fish. All catches were taken from the subtidal parts of the Furo do Meio near the sample site (max. 100 m distance). We used the U-test to compare catch parameters between day and night samples.

4 Results

4.1 Abiotic variables

Water temperature remained almost constant throughout the study period (28 ± 0.7 °C S.D.). Salinity dropped off remarkably from 30 psu early in February down to a minimum of 8 at the end of March. Salinities increased again in April (14 psu in April 29).

Mean water depth at the mouths of the intertidal creeks at HW was 1.6 ± 0.4 m ($n = 8$) at neaps and 2.7 ± 0.2 m ($n = 9$) at springs. Variability in maximum tidal height at neap tide was 16% higher than at spring tide. The weeks before equinox produced the lowest neap tide (1.1 m) and the highest spring tide (3.1 cm) (Table 1).

Due to wind force, maximum HW levels between two consecutive samples differed from 0.2 to 0.6 m in three sample pairs (No. 5 and 6; No. 13 and 14; No. 3 and 4). The two maximum neap tide HWs (No. 5 and No. 13) could be attributed to wind influence (Table 1).

4.2 Species composition in the intertidal creeks at high water

A total of 40 fish species (22 families) were captured at HW. The following seven families dominated by weight: Ariidae, Tetraodontidae, Auchenipteridae, Engraulidae, Mugilidae, Anablepidae, and Sciaenidae.

Eight species produced more than 85% of the total biomass: *Cathorops* sp. (34%), *Colomesus psittacus* (18%), *H. herzbergii* (10%), *P. nodosus* (6%), *Fenneropenaeus subtilis* (5%), *Anchovia clupeoides* (5%), *Mugil* spp. (4%), and *Anableps anableps* (4%) (Table 2).

Most abundant species were *F. subtilis* (28%), *Cathorops* sp. (17%), *Mugil* spp. (7%), *H. herzbergii* (7%), *P. nodosus* (7%), *C. psittacus* (7%), *Lycengraulis grossidens* (6%), and *A. clupeoides* (4%) of altogether 6142 individuals captured. All other species accounted for the remaining 17% of the total abundance, each with less than 2%.

Juvenile fish consistently accounted for 87% of the total catch. Mean TL and weight ± S.D. of all fish ($n = 4236$) was 9.1 ± 4.3 cm and 14.8 ± 28 g, respectively. Mean diversity H' was low (0.9 ± 0.1, range: 0.5 to 1.0).

Table 2. Total weight and total abundance of nekton species caught in 17 high-water block net samples in intertidal mangrove creeks, north Brazil, in the wet season 1999 ranked according to their total catch weight. Abund: Abundance. MC: Migratory categories (M: Marine migrants; E: Estuarine fish; F: Freshwater migrants). TC: Trophic categories (B: Benthophage; H: Herbivorous; I: Ichthyophage; B/I: Benthophage-ichthyophage; Z: Zooplanktivorous; L: Lepidophage). No vs. HW: significant positive correlations between the number of specimens and the maximum high-water level per sample are indicated; ** $p \leq 0.01$, * $p \leq 0.05$, (*) $p \leq 0.1$.

Species	Code	Weight (g)	Abund	Mean TL (min-max)	MC	TC	No vs. HW
FISH							
Cathorops sp. (Ariidae)	Ca	23 408	1030	12 (3-23)	E	B	**
Colomesus psittacus (Tetraodontidae)	Cp	12 081	417	7 (1-27)	E	B	*
Hexanematichthys herzbergii (Ariidae)	Hh	6312	441	10 (3-34)	E	B	
Pseudauchenipterus nodosus (Auchenipteridae)	Pn	3851	426	9 (5-13)	E	B	(*)
Anchovia clupeoides (Engraulidae)	Ac	3034	248	10 (5-17)	E	H	
Mugil spp. (Mugilidae)	Mu	2605	446	6 (2-29)	M	H	*
Anableps anableps (Anablepidae)	Aa	2320	75	13 (1-25)	E	H	
Lycengraulis grossidens (Engraulidae)	Lg	1354	348	7 (3-14)	M	Z	
Batrachoides surinamensis (Batrachoididae)	Bs	1025	4	20 (8-30)	M	B/I	*
Stellifer naso (Sciaenidae)	Sn	984	50	12 (6-14)	E	B	*
Stellifer stellifer (Sciaenidae)	Ss	788	89	7 (3-14)	M	B/I	(*)
Pterengraulis atherinoides (Engraulidae)		588	28	12 (2-20)	E	B/I	
Macrodon ancylodon (Sciaenidae)	Ma	553	46	8 (2-23)	M	B/I	(*)
Cynoscion leiarchus (Sciaenidae)	Cl	525	80	7 (2-16)	M	B/I	**
Cynoscion acoupa (Sciaenidae)		485	41	9 (2-19)	M	B/I	
Bairdiella ronchus (Sciaenidae)	Br	333	8	13 (7-18)	M	B	*
Stellifer rastrifer (Sciaenidae)	Sr	304	31	8 (3-14)	E	B	
Hyporhamphus roberti (Hemiramphidae)		283	35	12 (9-16)	M	Z	
Genyatremus luteus (Pomadasyidae)		280	30	6 (2-12)	E	B	
Micropogonias furnieri (Sciaenidae)		199	114	5 (3-9)	M	B	(*)
Oligoplites saurus (Carangidae)		197	97	5 (1-9)	M	L	
Achirus achirus (Soleidae)		167	4	13 (8-15)	E	B	
Lutjanus jocu (Lutjanidae)		143	2	(10-19)	M	I	
Guavina sp. (Eleotridae)		139	5	12 (10-14)	E	B	
Hexanematichthys passany (Ariidae)		138	1	24	M	B	
Centropomus parallelus (Centropomidae)		126	6	11 (11-14)	M	I	
Diapterus auratus (Gerreidae)		115	10	9 (7-13)	M	B	
Chaetodipterus faber (Ephippidae)		69	47	3 (1-7)	M	B	(*)
Cetengraulis edentulus (Engraulidae)		64	5	10 (6-14)	M	H	
Rhinosardinia amazonica (Clupeidae)		34	18	6 (4-7)	E	H	**
Anchoviella lepidentostole (Engraulidae)		26	20	4 (2-8)	M	H	
Anchoa spinifer (Engraulidae)		25	16	5 (4-8)	M	Z	
Cynoscion steindachneri (Sciaenidae)		25	1	14	M	B/I	
Odontognathus mucronatus (Pristigasteridae)		17	8	7 (5-9)	M	Z	
c.f. *Bryconamericus* sp. (Characidae)		8	1	9	F	Z	
Selene vomer (Carangidae)		7	2	(5-6)	M	Z	
Poeciliidae		3	2	(2-5)	F	Z	
Strongylura timucu (Belonidae)		1	2	(7-8)	M	TC	
Chloroscombrus chrysus (Carangidae)		0.6	1	3	M	Z	
Sphoeroides testudineus (Tetraodontidae)		0.1	1	1	M	B	
CRUSTACEA							
Fenneropenaeus subtilis (Penaeidae)	Fs	3321	1760	5 (1-14)			**
Palaemon northopi (Palaemonidae)		280	101	5 (3-8)			
Alpheus sp. (Alpheidae)		23	15	3 (2-6)			
Xiphopenaeus kroyeri (Penaeidae)		19	24	5 (4-6)			
Squilla sp. (Sqillidae)		8	1	9			
Nematopalaemon schmitti (Palaemonidae)		2	5	5 (4-5)			
Callinectes sp. (Portunidae)		-	3	-			
∑ Fish		62 613	4236				
∑ Crustacea		3653	1909				
∑∑		66 266	6145				

Estuarine fish, marine and freshwater migrants accounted for about 85%, 15% and 1% of the total catch weight, respectively (Table 2). Marine migrants dominated with 63% of the total species number while estuarine fish accounted for 32% and freshwater migrants for only 5%.

Benthophage fishes (77%) dominated the catch weight (Table 2). Herbivorous, bentho-ichthyophage, zooplanktivorous, ichthyophage, and lepidophage species accounted for 13, 5, 4, 0.4, and 0.3%, respectively. In contrast, benthophage fish species accounted only for 37% of the total fish species captured. Zooplanktivorous, herbivorous and bentho-ichthyophage accounted for 24, 17 and 15% of the total species number. Only two species were entirely ichthyophage (5%) and *Oligoplites saurus* was lepidophage (2%).

4.3 Biomass and density

Mean values of fish density and biomass of all species (± S.E.) were 0.19 ± 0.10 fish m^{-3} (range: <0.1 to 0.8) or 0.1 fish m^{-2} (range: <0.1 to 0.3) and 2.6 ± 0.7 g m^{-3} (range: 0.6 to 11.4) or 1.4 ± 0.3 g m^{-2} (range: 0.5 to 4.3), respectively.

Mean values of shrimp density and biomass were 0.1 shrimp m^{-3} (range: <0.1 to 0.3) and 0.1 g m^{-3} (range: <0.1 to 0.6) or 0.1 g m^{-2} (range: <0.1 to 0.2), respectively.

4.4 Life history

L_{50} of *A. anableps* was between 10 and 12 cm TL ($n = 75$; few specimens within the L_{50} range). L_{50} for *S. naso* was 10.7 cm ($n = 50$) and females predominated. L_{50} for *Cathorops* sp. was 13.6 cm ($n = 1030$). The size range of *P. northropi* (Table 2) indicated that the population was mainly composed by adults (Anger and Moreira 1998), 34% carried eggs. The length at which 50% of female *P. northropi* were carrying eggs was between 6.0 and 6.5 cm TL ($n = 101$). The population of shrimps *F. subtilis* in the creeks (mean TL: 5 ± 2 cm; $n = 1760$) was almost exclusively composed of juveniles or sub-adults as the TL of *F. subtilis* at first maturity is 8.3 and 7.2 cm for females and males, respectively (Lum Young et al. 1992). TL of *Xiphopenaeus kroyeri* at first maturity for females and males is 6.5 and 6.1 cm, respectively (Lum Young et al. 1992), indicating a population of mainly sub-adult specimens in the intertidal mangrove creeks (mean TL: 5 ± 1 cm; $n = 24$).

Male *Cathorops* sp. entered the mangrove creeks almost exclusively at spring tide, rather at night and rarely at daytime (5 to 20% of males in the catch). Ripe female *Cathorops* sp. were caught throughout the study period. Only one male *H. herzbergii* (33 cm TL) caught at SN was incubating embryos.

4.5 Stomach fullness

Cathorops sp. stomachs were constantly filled at least 50 to 75%. *Cathorops* sp. exhibited no periodicity in stomach fullness. *Cathorops* sp. fed especially on polychaeta, and small brachyuran crabs.
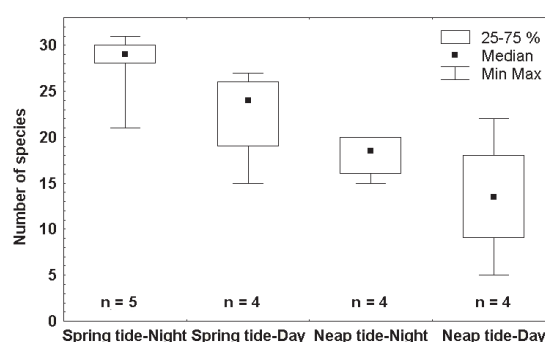

Fig. 2. Median number of nekton species captured at spring tide-night, spring tide-day, neap tide-night and neap tide-day in intertidal mangrove creeks at high water. The 25 to 75% quartiles and minimum and maximum values are shown.

Stomachs of *H. herzbergii* were generally 50 to 75% full throughout the samples. Stomachs were emptiest at NN ($p \leq 0.001$). Stomachs at ND and SD were fuller than at NN ($p \leq 0.05$ and $p \leq 0.05$, respectively), indicating a more successful feeding at daytime than at night. *Hexanematichthys herzbergii* mainly fed on small brachyuran crabs like *Uca* sp. and polychaeta.

Pseudauchipterus nodosus exhibited a marked day-night/spring-neap tide interaction ($p \leq 0.001$) with intense feeding at SN only. Stomachs of *P. nodosus* were fullest at SN and emptiest at SD ($p \leq 0.05$). Stomach fullness at neap tide was intermediate, but stomachs at night were again fuller than those at daytime. The stomachs contained hymenoptera, cicada, rests of chitin in general, small crabs and woodlouses that probably were captured in the mangrove forest.

Intestines of *C. psittacus* (the stomachs are usually empty; H. Keuthen, pers. comm.) in the intertidal creeks were generally full. The intestines contained barnacles and brachyuran crabs.

All mullets examined had an intestine darkened by ingested substrate, indicating iliophagous feeding in the creeks.

4.6 Temporal variations in assemblage structure

The number of species at spring tide was significantly higher than at neap tide ($p \leq 0.01$) (Fig. 2). The number of species at night was higher than at daytime ($p \leq 0.085$). The ratio of fish species to families (S/F) characterizing the diversity within families exhibited a similar pattern.

The mean total spring tide catch (5.7 kg) exceeded three times the catch at neap tide (1.9 kg) ($p \leq 0.01$). In creek A catches were significantly higher at night ($p \leq 0.05$), however, only due to extreme yields before equinox ranging between 0.3 kg and 10.3 kg at ND and SN, respectively (factor 38). Neither changes in biomass nor in density followed a significant pattern.

The assemblage structure of the catches differed in the species composition and the proportions between the species for SN, SD, NN and ND (Fig. 3). Catch weights of three fish species were higher at night than at daytime; and catch weight of nine fish and two crustacean species were higher at spring
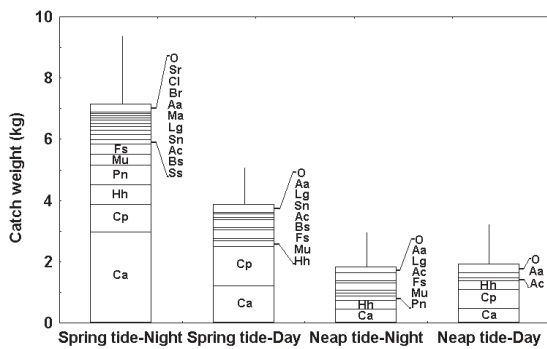
Fig. 3. Mean (±1 S.E.) catch weight of nekton species captured in intertidal mangrove creeks by block nets set at high water at spring tide-night ($n = 5$), spring tide-day ($n = 4$), neap tide-night ($n = 4$) and neap tide-day ($n = 4$). Stacked columns consider species contributing on average >0.05 kg to the mean catch weight. The species code letters are given in Table 2; O: Others.

Fig. 4. Multidimensional scaling (MDS) plot of 17 nekton samples taken in intertidal mangrove creeks in the wet season 1999, north Brazil. The mouth of the creeks was blocked at high water according to the factor combinations of tide and time of day: spring tide-night (SN), spring tide-day (SD), neap tide-night (NN) and neap tide-day (ND). The MDS grouped the nekton assemblages according to similarities between the catch weights for each species in each sample among all 17 block net samples. Previous to each factor combination is its respective sample number 1 to 17 (see Table 1). Two bold axis separate the plot in 4 quadrants where quadrant I contains nekton assemblages from SD, quadrant II from SN, quadrant III from NN and quadrant IV from ND. The clusters SN, SD and NN according to the dendrogram are encircled.

than at neap tide (Table 3). *Cathorops* sp., *H. herzbergii*, *A. anableps* and *A. clupeoides* were abundant throughout SN, SD, NN and ND. *Mugil* spp., *L. grossidens* and *F. subtilis* were rare only at ND. *Pseudauchenipterus nodosus* was abundant only at SN and NN. The only diurnal species was *C. psittacus*, being the dominant species at SD and ND while almost absent at NN (Table 3, Fig. 3). At neap tides, the daytime assemblage was a subset of the night assemblage. At spring tides, dominant species altered their proportions between day and night. Evenness J' differed significantly between SN, SD, NN and ND ($p \leq 0.05$). Species at NN were present more even than at the J' minimum at SN ($p \leq 0.01$). At SN, four species occurred with highest catch weights (*Cathorops* sp., *Rhinosardinia amazonica*, *Anchoa spinifer*, *Stellifer stellifer*), ichthyophage fish species (e.g. *Batrachoides surinamen*sis, *Macrodon ancylodon*, *Bairdiella ronchus*, *C. leiarchus*, *Stellifer* spp.) and Sciaenidae were especially abundant (2-way ANOVA; tide: $p \leq 0.01$; time of day: $p \leq 0.05$). Diversity did not differ significantly between creeks and treatment combinations.

The combination of "tide" and "time of day" had a significant effect on the composition of the fish assemblage structures in the intertidal mangrove creeks (2-way cross-ANOSIM, tide: $p \leq 0.001$; time of day: $p \leq 0.01$) as displayed in the MDS ordination (Fig. 4). Catches at SN were grouped in quadrant-II (upper left), those at SD in quadrant-I, those at NN in III and those at ND in IV. Daytime catches were arranged in quadrant-I and IV. Night catches were arranged in quadrant-II and III. Quadrant-I and II contain spring tide catches and quadrant-III and IV contain neap tide catches. The distances between subsequent samples increased towards the lower margin, indicating that subsequent samples at spring tide (upper quadrants) had less variable species compositions than samples taken at neap tide (Fig. 4).

We may use sample No. 13 (highest neap tide HW) and No. 14 to illustrate a possibility that wind-induced changes in HW level may have been reflected in the composition of the fish assemblages (Figs. 4 and 5a, Table 1). No. 13 (ND) had a wind-induced 55 cm higher HW and was assigned to the SD group (1st instead of 4th quadrant). The subsequent No. 14 (NN) was assigned to the NN group. Likewise, the
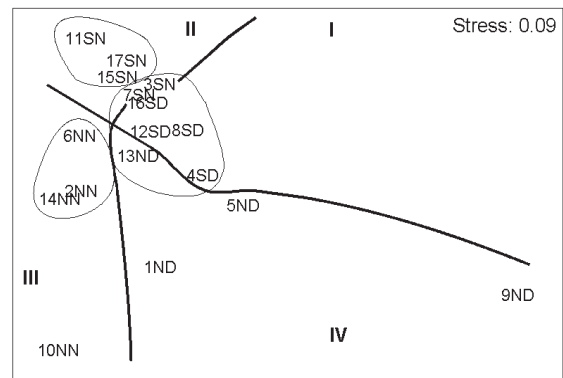
lowest spring tide-HW No. 4 (SD) yielded an almost ND-like fish assemblage (close to 4th quadrant) whereas the previous No. 3 (SN) with 25 cm higher HW level was assigned to the SN group. However, apparently no response in assemblage structure occurred at No. 5 (ND) where wind caused a 22 cm higher HW level compared to subsequent No. 6 (NN).

The abundance per species in the repetition trial No. 16/No. 17 was significantly higher at SN (second sample) than at SD (first sample) (10 species; $p \leq 0.001$), suggesting unbiased immigration from one tide to the next. Accordingly, the samples 16 and 17 yielded different assemblage characteristics typical for SD and SN (Fig. 4).

The superimposed circles show that HW level (Fig. 5a) had a clear impact on the fish assemblage structure while salinity and water temperature had not (Figs. 5b,c).

The numbers of 14 species correlated positively with HW level (Table 2). Consequently, total weights and abundance of fish ($p \leq 0.001$) and shrimp ($p \leq 0.01$) correlated positively with HW level; the higher the HW level of a tidal cycle in the mangrove creeks was, the more fish and shrimp entered. This relationship for fish and shrimp was best described by a power function (weight fish: $y = 2 \times 10^{-6} \, x^{2.6678}$, $R^2 = 0.70$; shrimp: $y = 5 \times 10^{-7} \, x^{3.6242}$, $R^2 = 0.55$).

The four moon phases had no apparent influence on the grouping of the species assemblages in Figure 4 (see together with Table 1). Longer-term changes were detected only for *Anchoviella lepidentostole* where abundance increased with decreasing salinity ($p \leq 0.05$).

Table 3. Results of 3-way ANOVA (n = 16; No. 1-16) for catch weights of 23 species with $n > 10$ specimens calculated as a mixed model ANOVA, creek being the unplanned factor. Only significant species are shown. * $p \leq 0.05$; trend $p \leq 0.1$. Significance for "Tide" means: Spring tide > Neap tide; significance for "Time of day" is indicated with (D) for "higher catches at daytime than at night" and (N) for "higher catches at night than at daytime"; Creek: Creek A and creek B. Interactions are explained below (see i-viii).

Species	Treatment			Interaction			
	Tide	Time	Creek	Tide vs. Time	Tide vs. Creek	Time vs. Creek	Tide vs. Time vs. Creek
A. anableps							* (i)
Cathorops sp.	trend			* (ii)	trend (iv)	* (iii)	
O. saurus							* (i)
R. amazonica	*	trend (N)					
A. clupeoides		* (N)					
A. spinifer	* (v)	* (v)		* (v)			
C. faber	*						
Mugil spp.	trend						* (i)
C. leiarchus	*			trend (vii)		* (vi)	
M. ancylodon	*						
M. furnieri	*						
S. stellifer							* (v)
C. psittacus	trend	* (D)		trend (viii)			
F. subtilis	*						
Alpheus sp.	trend						

(i) The multiple interactions cannot be explained.

(ii) At spring tide, catches at night were higher than those at daytime; at neap tide catches at night were only slightly higher than those at daytime.

(iii) Creek A yielded higher catches at night than at daytime. Creek B yielded lower catches at night than at daytime.

(iv) At neap tide, creek B yielded almost as low catches as did creek A; at spring tide, however, creek B yielded clearly higher catches than creek A.

(v) This species only occurred at spring tide-night in creek A.

(vi) In creek B, catches were higher at night than at daytime. In creek A catches were lower at night than at daytime.

(vii) At spring tide, night catches were only slightly higher than catches at daytime. At neap tide the difference between day and night was highly pronounced.

(viii) At neap tide, night catches were insignificant whereas the other three factor combinations yielded almost equal catches.

4.7 Species composition in the subtidal zone at low water

A total of 25 species were caught in the subtidal parts of the Furo do Meio main channel at LW (Table 4). The mean number of fish species, catch weight, abundance, eveness J' and diversity H' ($\pm$ S.E.) was 7 $\pm$ 1, 0.7 $\pm$ 0.3 kg, 52 $\pm$ 22, 0.5 $\pm$ 0.1, 0.4 $\pm$ 0.1, respectively. The parameters lacked any statistical difference between daytime and night samples.

However, the fish assemblage structure based on catch weights differed significantly between day and night (1-way ANOSIM, $p \leq 0.01$), suggesting a uniform species composition with changing proportions. Cluster and MDS essentially separated night catches with heavy schools of *Cetengraulis edentulus* (N1, N7, N8) from daytime samples (Fig. 8).

Cetengraulis edentulus accounted for 64% of the total catch weight. Consecutive samples were often grouped far from each other, suggesting high spatial variability and a patchy fish distribution at LW.

Shrimp were abundant and exhibited a wide range in size (Table 4). Mean values of fish density and biomass were 1.4 $\pm$ 0.4 fish m^{-2} and 30 $\pm$ 14 g m^{-2}, respectively. Mean shrimp biomass was 2.1 $\pm$ 0.3 g m^{-2}. Biomass values of fish in the Furo do Meio main channel at LW were 22 times higher and the shrimp biomass was 27 times higher than in the adjacent intertidal mangrove creeks at HW.

The catches near to the shallow channel banks yielded mainly juvenile fish whereas larger fish (*H. herzbergii*, *Cathorops* sp.) were usually caught only when the seining covered deeper areas and/or when it passed near to branches or

Table 4. Abundance of species caught at low water using a scientific (12 mm stretched mesh size; daytime and night, neap tide in August in the early dry season 2002; $n = 16$) and an artisanal beach seine (60 mm stretched mesh size; daytime at neap and spring tide in October 2000 in the dry season) in the Furo do Meio main channel, north Brazil.

Species	Scientific beach seine		Artisanal beach seine	
	N	Mean TL (min-max)	N	Mean TL (min-max)
C. edentulus (Engraulidae)	519	11 (7-12)		
H. herzbergii (Ariidae)	144	10 (5-34)	60	31 (27-50)
A. achirus (Soleidae)	28	4 (3-9)	4	20 (15-23)
C. psittacus (Tetraodontidae)	28	3 (2-7)		
P. atherinoides (Engraulidae)	23	8 (7-12)		
S. naso (Sciaenidae)	21	9 (7-12)		
Symphurus plagusia (Cynglossidae)	20	4 (3-9)		
Citarichthys spilopterus (Bothidae)	15	6 (4-10)		
B. surinamensis (Batrachoididae)	8	13 (9-15)	7	36 (28-41)
Cynoscion spp. (Sciaenidae)	8	5 (4-5)		
Cathorops sp. (Ariidae)	6	13 (10-16)		
S. stellifer (Sciaenidae)	6	9 (8-10)		
M. furnieri (Sciaenidae)	4	6 (4-11)		
O. saurus (Carangidae)	4	7 (6-10)		
S. vomer (Carangidae)	4	8 (6-10)	1	20
Mugil spp. (Mugilidae)	3	7 (7-8)	1	39
A. anableps (Anablepidae)	2	(6-7)		
G. luteus (Pomadasyidae)	2	(4-5)		
Guavina sp. (Eleotridae)	1	10		
Caranx sp. (Carangidae)	1	3		
D. auratus (Gerreidae)	1	6		
S. testudineus (Tetraodontidae)	1	3		
Diodontidae	1	3		
Epinephulus itajara (Serranidae)			1	24
F. subtilis (Penaeidae)	252	6 (3-14)		

trunks (Table 4). The artisanal catches covering deeper parts of the main channel, were very efficient and caught exclusively large-sized fish (Table 4). The artisanal catches showed no difference between spring and neap tide. *Cathorops* sp. was absent from the artisanal catches because they escape through the large mesh size (pers. comm. with fishermen).

5 Discussion

Block netting in intertidal creeks is an inexpensive method with a high catch efficiency (Bozeman and Dean 1980). In our study some fish could have escaped to adjacent creeks during high inundation levels, but since high spring tides produced extremely high catches such bias is probably negligible.

The low habitat diversity limits the number of fish species inhabiting tidal mangrove creeks; Davis (1988) caught thirty-eight fish species in Australia, Wright (1986) only nine in Nigeria. However, we caught a similar number of species and families in two months that Barletta et al. (2003) caught with monthly sampling over one-year at ND in three 1st order creeks of the Furo do Meio. This can mainly be attributed to the sample design that covered SN, SD, NN and ND more

completely. Apparently highly mobile ichthyofauna in tidal areas exhibits very dynamic short- to medium term changes in assemblage structure that are comparable to the annual variability in species composition.

The repeated samplings suggest that at each tide, fish and shrimp re-colonize the intertidal mangrove creeks. Apparently, creek preference on the level of 2nd order intertidal creeks is not a common behavior. However, multiple repetitive sampling in the same creek negatively affects fish abundance (Kleypas and Dean 1983; Rönnbäck et al. 1999; own obs.).

5.1 Biomass and density

Mean values of fish density and biomass at HW were close to the annual mean of 0.1 fish m^{-2} or 2.1 g m^{-2} as determined by Barletta et al. (2003). Density and biomass lacked any significance due to high variance. Compared to values from Australia (Robertson and Duke 1990) and a usual range of fish biomass in tropical and subtropical estuaries of 5 to 15 g m^{-2} (Blaber 1997, p. 107), the biomass in our mangrove creeks is low. The biomass flow through the fish compartment of the Caeté mangrove estuary is of low importance for the trophic
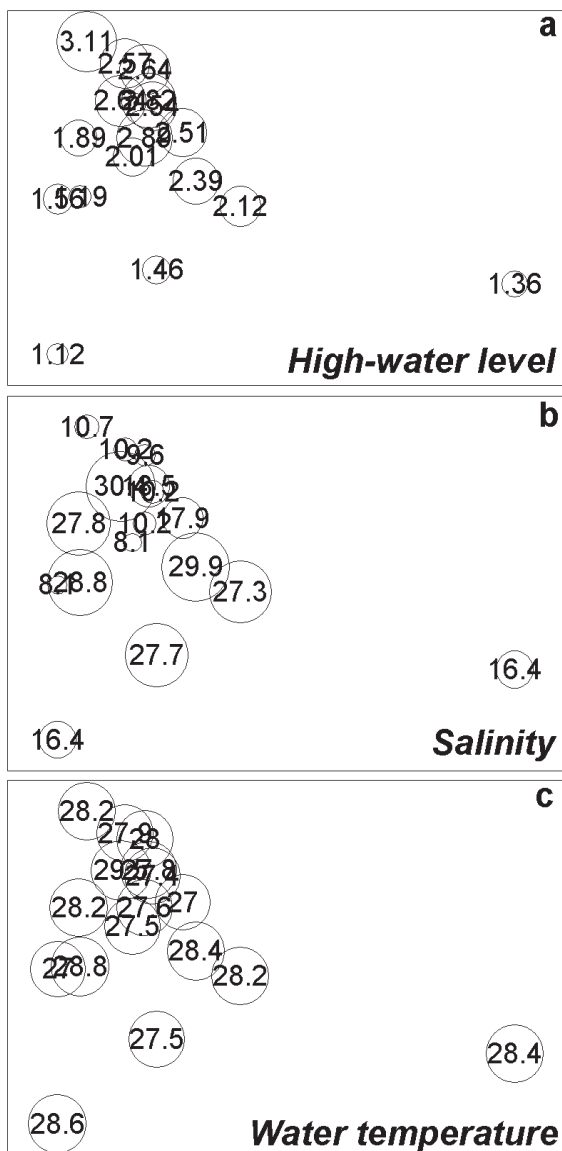
Fig. 5. The same MDS as in Figure 4, but with superimposed circles, sized according to changes in high-water level (a), salinity (b) and water temperature (c). Abiotic values are also given in Table 1.

Fig. 6. Cluster and MDS plot of eight daytime (D) and eight night (N) beach seine hauls at LW in the subtidal parts of the Furo do Meio at neap tide in August 2002 (early dry season). Three groups and two single samples were separated at 47% similarity.

5.2 Trophic relations and residence status

The importance of detritus-based food chains in mangroves is emphasized by our result that benthophage fish species produced 77% of the total catch weight. Koch (1999) and Koch and Wolff (2002) found the highest number of epibenthos organisms in the intertidal mangrove creeks where the benthos is rich in *Uca* spp. (Koch 1999; Koch and Wolff 2002), polychaeta (Acheampong, pers. comm.) and oligochaeta (Dittmann 2001). This agrees with studies from Florida and Australia that show food webs of mangrove systems to be based on detritus consumption (Odum and Heald 1972; Blaber 1997, p. 176).

Like in other tropical estuaries (Blaber 1997, p. 46), marine migrants were the largest group in our study (63%). However, 32% of estuarine fish species produced 84% of the total catch weight, emphasizing the important ecological role that estuarine fish species play in the Caeté mangrove system. In mangrove creeks in tropical Australia, 41% of estuarine fish species produced a total biomass share of only 43% (Blaber et al. 1989).

Tidal migrations of fish represent a principal means of energy transfer from intertidal to subtidal areas and towards the sea. Tidal-migrating estuarine fish like *Cathorops* sp., *C. psittacus, A. anableps, B. surinamensis* and *S. naso* that spend their entire life in the mangrove environment have the main share in total fish biomass. Hence, considerable quantities are not exported due to large-scale seasonal emigration

flow within the mangrove system because extensive material export only occurs at spring tides (Wolff et al. 2000). The nekton biomass in the mangrove creeks was mostly produced by high numbers of small fish. Moreover, while weak neap tides may not suffice to support the growth of a more productive intertidal fauna and flora, strong spring tide currents transporting massive quantities of inorganic sediment, may restrict the growth of e.g. an extensive filter feeding fauna in the mangrove creeks that again could support a higher nekton biomass. Additionally, the strong tidal mixing and low turbidity restricts the pelagic phytoplankton production (Wolff et al. 2000).
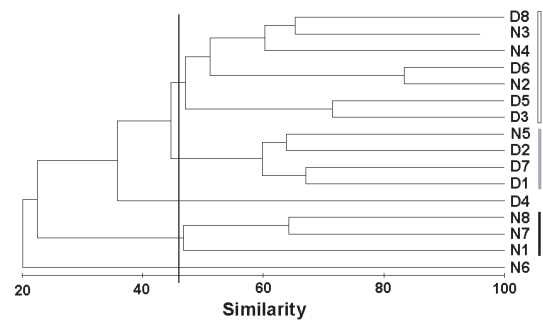
as proposed by Bozeman and Dean (1980) and Weinstein et al. (1980) for the temperate US east coast, but rather remain in the mangrove estuary system. Transients like mullets, shrimp and predatory Sciaenidae and Carangidae may feed intensively, thereby exporting biomass to the sea. However, their wet season share in the total biomass was low. In New Caledonia were resident species usually at low trophic level and only transient species contributed to net export of energy to coastal waters (Thollot et al. 1999).

As many species emigrate with filled stomachs, feeding is considered a principle function for fish immigration into the mangrove creeks, thus transferring energy from intertidal to subtidal mangrove areas only.

According to Leal-Flórez (pers. comm.) and Oliveira-Santos (pers. comm.), *Cathorops* sp. is a polychaete-eater (Blaber et al. 1994), also feeding on vegetal material, copepods, crabs and diatoms. The dominance of *Cathorops* sp. in the mangrove creeks is probably closely related to the specialized feeding on abundant polychaeta and special adaptations like mouth-breeding and the arming with lateral and dorsal spines.

The occurrence of buccal-incubating male *Cathorops* sp. mainly at SN was certainly not related to feeding migrations but likely linked to avoidance of nocturnal predation. Rountree and Able (1993) suggested that nocturnal immigration of *Menidia menidia* in salt marsh creeks was caused by avoidance movements related to the presence of predators.

Brenner (unpubl. data) found *H. herzbergii* feeding on *Uca* sp., Grapsidae, Gamaridae, *Eurytium limosum*, athropoda, polychaeta (Capitellidae, Nereidae) and snails (Littorinidae, Mytelidae); SD provided the best conditions for feeding of *H. herzbergii* which might be linked to diurnal activity patterns of the brachyuran crab species in the mangrove creeks (Koch 1999).

In the dry season, about 70% of *C. psittacus* emigrated intertidal mangrove creeks with medium to totally filled intestines. The principal food items were Balanidae, brachyuran crabs, teleostei, bivalves, insecta, and polychaeta. The diurnal activity pattern of *C. psittacus* is probably related to a fairly visual search for prey and the fact that all *Uca*-species are diurnal and cease feeding in the evening (Koch 1999). Stomachs of intertidal *C. edentulus* were uniformly full, mainly with diatoms (Keuthen, unpubl. data).

Brenner and Krumme (2004) found that *A. anableps* feed on red algae, Insecta, and Grapsidae. Best foraging conditions for *A. anableps* occurred at SD when daylight and maximum intertidal accessibility coincided. Insecta occurred in the stomachs of intertidally foraging *A. anableps* (Brenner and Krumme 2004), *P. nodosus* and *C. psittacus* (Keuthen, unpubl. data) and were also found in the stomachs of different fish species in Australia (Robertson 1988), suggesting that Insecta may provide an important protein source in some intertidal mangrove fish species.

Anchovia clupeoides clearly entered the creeks to feed. Although Brenner (unpubl. data) caught more *A. clupeoides* at daytime than at night, stomachs were fuller at night (more copepoda) than at daytime (more diatoms). Since abundance of both phytoplankton (Schories, unpubl. data) and zooplankton (Krumme and Liang 2004) in the Furo do Meio are highest

at spring tide and essentially lack a significant diel cycle, their nocturnal immigration at spring tides can be readily explained by feeding migrations.

5.3 Tidal and diel variations in species composition

The interplay of the spring/neap tide pulse together with the superimposed impact of the day/night cycle significantly determined fish assemblage compositions. The tide determines the habitat accessibility for tidal migrating fish species while the diel cycle controls the visual conditions and diel changes in the organisms' activity. However, the tide had a stronger influence on the catch weights and assemblage compositions than the diel cycle.

The numbers of species and the S/F ratio showed that more niches were available at spring tide. This is likely linked to greater habitat accessibility and food availability at spring tides, e.g. in zooplankton (Krumme and Liang 2004).

Although the influence of the tidal and diel cycle on the movements of tidal migrating fish is well established (Gibson 1988), we present evidence for distinct assemblages resulting from such movements. Brenner (unpubl. data) repeated our sample design in two 1st order creeks of the Furo do Meio in the wet season 2001 and found the same interplay of tide and time of day, underlining that this pattern recurs annually, and most likely even is a typical fortnightly feature of the system year-round. Schaub (unpubl. data) analyzed the early dry season catches of tidal-migrating fish in large commercial tidal traps in the Caeté bay. Catches were higher at night than at daytime with night assemblages dominated by Ariidae and Sciaenidae whereas daytime assemblages were more diverse in terms of family composition. Interestingly, he observed a pronounced species shift from neap to spring tide (wax to full moon), with species proportions changing one day before full moon. Laroche et al. (1997) and Lin and Shao (1999) observed similar temporal assemblage changes.

The lunar cycle is likely of minor importance in the mangrove ichthyofauna. In the wet season, minimal water clarity and heavy clouding may severely limit the impact of lunar light levels to control fish behavior. Quinn and Kojis (1981) also found no significant differences between full and new moon in nocturnal fish assemblages in subtropical Australia.

Seasonal salinity alternations are reflected in longitudinal changes in the structure of the fish communities in the Caeté estuary system (Barletta 1999, p. 83). However, almost all fish living in tropical estuaries are euryhaline (Blaber 1997, p. 125) and short-term salinity changes – even though severe – may not cause major disturbances in the structure of tropical estuarine fish communities. Variations in water temperature were already recognized as insignificant in triggering changes in the fish community (Barletta-Bergan et al. 2002a,b).

5.4 Tidal migration

The tide based on the lunar cycle is modified by topographical, meteorological (wind, atmospheric pressure) and hydrological phenomena. Species composition structures at spring tides are more similar and can be attributed to less variable

HW levels at spring than at neap tide (Table 1). We conclude that at spring tides, the strong currents lead to a more homogenous species structure, whereas at neap tides, when the creek environment is less subjected to harsh environmental conditions, the species composition becomes more heterogeneous.

Spatio-temporal movements are closely linked to the accessibility of resource-rich intertidal habitats. The topography of the plateau mangrove of the Caeté estuary results in a 51% increase in inundated mangrove area with just a 4% water level increase above mean HW (Cohen et al. 2000). Like Robertson and Duke (1990), we observed that extreme HW levels produced exceptionally high catches. Moreover, the maximum HW level also had a clear influence on the structure of the fish assemblages (Fig. 5a). Movements of the fish community also depended on tidal height in Laegdsgaard and Johnson (1995) and Davis (1988). Water height or the requirement of a minimum water level seem to be important for the occurrence of certain fish species in shallow-water environments, especially in piscivorous fish (Davis 1988; Blaber et al. 1995; Laroche et al. 1997).

The maximum HW level is an important parameter because it captures the accessibility of the intertidal area. It is generally agreed that fish perceive pressure changes (Gibson 1973). Gibson proposed the selection and maintenance of a particular depth range by a fish species throughout the tidal cycle, thereby functioning as a possible mechanism to control the tide-related movements and size-depth relationships. Our results suggest that with increased HW levels, indicative of extreme flooding of the mangrove, fish respond with increased immigration.

Fish species resident in the intertidal mangrove zone (Barletta et al. 2000) did not move over larger distances in their tidal migration (Horn et al. 1999). In contrast, almost all species caught in the subtidal parts of the Furo do Meio at LW were also present in the intertidal mangrove at HW. Barletta (1999) caught thirteen species in the subtidal parts of the Furo do Meio at ND, the majority of which were again caught in the intertidal mangrove at HW (*Cathorops* sp., *C. psittacus*, *A. clupeoides*, *G. luteus*, *Mugil* spp., *C. acoupa*, *P. atherinoides*, *H. herzbergii*, *A. anableps*, *S. naso*). This suggests migration between the two habitats over the distance of at least several 10 to 100 m.

It can be assumed that the fish returning from the intertidal feeding grounds split their routes towards the subtidal zone both inter- and intraspecifically; e.g. juvenile and adult *C. psittacus* co-occurred at HW, but not one adult specimen was caught at LW in the subtidal parts of the Furo do Meio. However, the adults were frequently caught in tidal traps in the Caeté bay at ebb tide. It is still unknown where the fish stay when they are absent from the flooded mangrove creeks at HW. Such larger-scale tidal migrations (probably several km per tide) also take place in species like *C. edentulus*, *M. ancylodon, C. acoupa* and *Mugil* spp. (pers. comm. with fishermen). Schools of *C. edentulus* that constantly become trapped in the tidal tributaries during ebb tide as indicated by the beach seine catches, the low catch efficiency of the beach seine (net avoidance) and the large fish caught by artisanal seining in the deeper subtidal zone indicate that our

LW biomass values are likely underestimations of the huge biomass that agglomerates in the main channels.

Significant diel changes in the fish assemblage structure at LW confirmed the distribution patterns observed at LW using shallow-water sonar (Krumme and Saint-Paul 2003). At LW, juvenile fish were abundant in shallow water whereas larger fish withdraw to deeper areas and close to wooden debris at LW. This distribution may likely be an effort by juveniles and shrimp to avoid predation from larger fish (Clark et al. 2003). Further, juvenile fish may feed on zooplankton that is close to the surface at LW (Krumme and Liang 2004). Finally, staying in shallow waters close to the channel bank at LW may facilitate an early immigration into the intertidal zone for the juveniles at the start of the flood tide (Krumme and Saint-Paul 2003; Brenner and Krumme 2004; Krumme 2004). In tropical Australia, *Penaeus merguiensis* were concentrated in the main channel in the turbid shallows near the banks from where they entered the mangrove creeks during flood tide (Vance et al. 1990). A similar distribution of shrimp is exploited in north Brazil by artisanal fishermen that hand-trawl for shrimp, mainly *F. subtilis*, in the muddy upper reaches of the mangrove channels during nocturnal LW, especially during the dry season when shrimp abundance is higher (pers. comm. with fishermen).

5.5 Piscine predation

We have evidence to assume that there is reduced nekton mortality during foraging in the shallow submerged creeks. Ichthyophage fish were almost completely absent from the intertidal mangrove creeks, except at SN when light levels are lowest. The fish still feed efficiently on their prey even under high turbidity conditions and low light levels (Grecay and Targett 1996). Predominance of nocturnal feeding of piscivorous fish was demonstrated by Kleypas and Dean (1983) and Blaber et al. (1995). However, the ichthyophage fish were usually small-sized juveniles, hence unlikely to prey upon similar sized juveniles of other species. The stomach fullness of the few larger ichthyophage specimens was highly variable and only about 25 ± 18% S.D. had at least one prey item in their stomach.

An almost complete absence of piscivorous fish is a common feature of shallow-water habitats (Blaber 1980; Ruiz et al. 1993; Rönnbäck et al. 1999; Paterson and Whitfield 2000). In the creeks, predatory fish preyed upon Mugilidae, *R. amazonica* (Clupeidae), *A. spinifer* (Engraulidae) and especially *F. subtilis*. Shrimp, due their numerical abundance and the wide spectrum of available sizes, were of special importance as prey items for predatory fish. Both predators and their prey were more abundant at spring tides (Table 2; Fig. 3), suggesting (i) that the tide synchronized abundance patterns in the predators and their prey and (ii) that predators are fairly unspecific feeders and feed on what is abundant (Blaber 1986).

6 Conclusion

The intertidal mangrove creeks provided an important nursery habitat for juvenile fish and shrimp at HW. The fish

extensively fed in this habitat and likely experienced reduced predation due to the almost complete absence of larger-sized piscivores.

Benthophage estuarine fish dominated the intertidal mangrove ichthyofauna, indicating a predominantly detritus-based food chain and suggesting that considerable biomass remains in the mangrove system.

The HW-nekton assemblages at SN, SD, NN and ND were significantly different in their species compositions, indicating that the interplay between tide and time of day determined the tide-related movements of fish and shrimp. The tide is the principal pulse of the mangrove system, synchronizing changes in abundance of fish, shrimp, zooplankton (Krumme and Liang 2004), detritus export (Schories et al. 2003) and biogeochemical parameters (Dittmar and Lara 2001). The strongest exchange between aquatic system compartments most likely occurs at spring tides when abundance, richness and assemblage complexity of the nekton were greatest.

Species-specific studies on tidal-related patterns in feeding showed that the interaction of HW height and time of day influence the degree of foraging success of the fish (Brenner and Krumme 2004).

Higher submergence levels lead to a higher influx of tidally migrating fish.

At LW, fish concentrated in the subtidal parts of the channel. The LW species structure essentially was a less diverse subset of the assemblage caught in the intertidal mangrove creeks at HW. This indicates that not all species and sizes reside at LW near the areas where they feed at HW and that hence, fish split the routes of migration at ebb tide to return to a specific LW habitat. Thus, the foraging ranges, destinations of travel and depth distributions of fish movements may not only differ interspecifically, but may also ontogenetically change while juveniles grow to adults (Gillanders et al. 2003).

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