Journal of Fish Biology (2007) **70,** 406–427
doi:10.1111/j.1095-8649.2007.01313.x, available online at http://www.blackwell-synergy.com

Tidal migration and patterns in feeding of the four-eyed fish *Anableps anableps* L. in a north Brazilian mangrove

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(Received 21 December 2005, Accepted 27 September 2006)

The tidal migration, temporal and spatial patterns in feeding of the surface-swimming four-eyed fish *Anableps anableps* (Anablepidae) were studied in a macrotidal mangrove area in north Brazil to exemplify the ecology of a tropical intertidal fish. Visual censuses in the main channel showed that abundances were high at low water (LW) and low at high water (HW). *Anableps anableps* entered the intertidal creeks with the first flood rise. They fed in the inundated mangrove at HW and returned gradually after the ebb current maximum to concentrate again in the subtidal parts of the main channel at LW. This pattern occurred at neap, mid and spring tides throughout the year. The tidal migration was triggered by water level, not by time. In the study area the diet of *A. anableps* caught with block nets was dominated by intertidal red algae (*Catanella* sp.). Other important food items were Insecta and Grapsidae. The combination of high inundation and daylight (spring tide-day) provided the best foraging conditions, probably emphasizing the importance of the above-water eye. Darkness and low inundation was linked to poorest foraging conditions (neap tide-night). The quantity of food consumed by *A. anableps* was clearly influenced by the factors tide, time of day and creek location, but not by size and sex. The qualitative composition of the diet was not influenced by any of the factors, except for mud, which was only ingested at neap tides. The temporal and spatial variability in food consumption suggests that food web modelling in macrotidal areas may lead to misinterpretations of the overall systems dynamics if the spring and neap tide alternation and the diurnal cycle are not considered.

Key words: *Anableps anableps*; mangrove creek; mutualism; stomach fullness; tide; visual census.

INTRODUCTION

The four-eyed fish *Anableps anableps* (L.) (Anablepidae) is a viviparous cyprinodontiform that has long attracted the attention of scientists. This fish species always swims at the water surface and its eye is divided horizontally into an upper and lower half by a band of opaque tissue, thus enabling *A. anableps* to have simultaneous vision in air and water (Sivak, 1976). In the

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international aquarium trade, *A. anableps* is a well-known species and behavioural studies have been conducted in captivity (Mattig & Greven, 1994*a*, *b*).

Anableps anableps inhabit mangrove environments along the north-east coast of South America. The general ecology of this unique fish species, including detailed quantitative assessments of feeding habits in its natural environment, still remains largely unknown (Miller, 1979; Ribeiro & Castro, 2003). Wothke & Greven (1998) have described *A. anableps* from the Trinidad region as feeding in exposed flat mud banks during ebb tide, and consuming algae and arthropods that were occasionally captured by a leap into the air. Zahl *et al.* (1977) observed *A. anableps* at the Surinam River feeding on mud on the exposed shoreline at low water. Other food items are not mentioned.

Anableps appear to undertake regular intertidal migrations. Schwassmann (1967, 1971) observed *Anableps microlepis* Müller & Troschel exhibiting a regular tidal periodicity following the semi-diurnal tidal regime and the fortnightly alternation between spring and neap tides in a coastal lagoon in Salinópolis (Pará, Brazil); *A. microlepis* moved up onto the beaches each rising tide, day or night. Wothke & Greven (1998) observed *A. anableps* moving with the tidal edge (microtidal regime) during field trips in Trinidad. In fishes that undertake regular intertidal migrations, feeding is an important aim, in addition to the avoidance of predators and competitors, and the selection of appropriate environmental conditions (Gibson *et al.*, 1998). In north Brazil macrotides pulse the patterns of inundation in the intertidal zone. For example, on the coast of Pará, a tidal range of 2–3 m at neap tide and 3–4 m at spring tide (in the mangrove habitat) causes significant changes in accessibility to intertidal fauna on both vertical and horizontal scales that may significantly alter patterns of consumption and diet composition of the fishes. This dynamic may again have important consequences for estimates of fish biomass and density, and finally for trophic modelling that relies on a predator–prey matrix and the consumption per unit of biomass (Wolff *et al.*, 2000).

Weisberg *et al.* (1981), Weisberg & Lotrich (1982) and Hampel & Cattrijsse (2004) have investigated the tidal and diurnal influence on food consumption by fishes from salt marshes, but there are no detailed studies linking tidal migration and feeding of fishes from mangrove environments. This may partially be due to the high turbidity that hampers the direct observation of the movements and behaviour of the fishes. Furthermore, studies in tidal environments require a high sample resolution that conventional fishing methods usually cannot provide. Additionally, strong tides and the structural complexity of the mangrove habitat often limit their use (Horn *et al.*, 1999).

The surface-swimming behaviour of *A. anableps* provides a unique opportunity to visually track their movements during a tidal cycle in the mangrove environment. Taking advantage of this behavioural pattern, the tidal migration and the feeding of *A. anableps* was studied to better understand the ecological role this fish plays in a mangrove system in north Brazil. The aim of this study was to determine (1) whether abundances of *A. anableps* changed with tide (spring and neap tide), time of day (day and night), sample site (two mangrove creeks) and during tidal cycles, and (2) whether tide, time of day and sample site influenced diet composition.

MATERIALS AND METHODS

STUDY AREA

The study area was located within the world's second largest mangrove area, *c.* 300 km south-east of the mouth of the Amazon River (Kjerfve & Lacerda, 1993). The study was conducted in the macrotidal blind ending channel Furo do Meio, a tidal tributary of the Caeté Bay, situated north of Bragança (Pará, Brazil) (Fig. 1). The Furo do Meio is *c.* 4·5 km long, draining the central part of a 180 km^2 mangrove peninsula dominated by *Rhizophora mangle* L., intermixed with *Avicennia germinans* L. at more elevated sites.

In the muddy upper reaches of the Furo do Meio, the main channel width is *c.* 50 m at high water (HW) and *c.* 30 m at low water (LW). At LW, only the main channel holds water. The rest of the branching network of first, second and third order creeks that channel the tidal flow into the mangrove is intertidal and essentially empty at LW, except for a degree of seepage water from mangrove sediments in the thalwegs.

In the lower reaches of the Furo do Meio, channel width is 400 m at HW. At LW, however, it is only *c.* 30 m wide and in the main channel large sand banks are exposed to the air. The tidal environment is characterized by a rapid water level rise at flood tide ('first flood rise') (Krumme, 2004). Maximum flood current speeds can exceed 1·5 m s^{-1} at spring tide and are usually <0·5 m s^{-1} at neap tide (U. Krumme, unpubl. data).

The tide is semi-diurnal and asymmetric; flood and ebb tide last 4 and 8 h, respectively. During the last 4 h, the ebb tide is extremely weak with an almost negligible fall in the water level. Water temperatures range between 25 and 31° C. Salinity in the Furo do Meio can fall below 5 in the wet season (January to June) and exceed 35 in the dry season (July to December). Annual Secchi disk depth range is between <5 and 100 cm at neap tide and <5–40 cm at spring tide, respectively. During a tidal cycle, Secchi disk depth maximum occurs around HW (U. Krumme, unpubl. data).

CENSUSES

Every 15 min during daylight (0600–1800 hours), the *A. anableps* present in a channel section of the upper reaches of the Furo do Meio were counted both with and without binoculars (10 × 40). As the fish quickly dart away from the light of torches, they were not counted at night. Nine diurnal cycles, six in the dry season 2002 and three in the wet season (one in 2001, two in 2003), were sampled. Wet season censuses accompanied the hydroacoustic sampling of Krumme & Saint-Paul (2003) and were conducted in section 1 (length: 40 m; width at LW: 30 m), counting from the southern edge of the mangrove plateau (Fig. 1). Dry season censuses accompanied the hydroacoustic sampling of Krumme (2004) and were carried out in section 2 (length: 36 m; width at LW: 30 m) from a bridge crossing the Furo do Meio *c.* 500 m upstream from section 1 (Fig. 1). Each section covered a rectangular area marked off by visible landmarks. A total of 397 counts were conducted ($n = 262$ in the dry season, section 2; $n = 135$ in the wet season, section 1). The theoretical number of 432 counts (12 h × 4 counts h^{-1} × 9 censuses) was not attained because one field campaign was stopped early.

Anableps anableps were usually distributed in groupings, which were generally not further than 1 m away from the water edge on both banks throughout the tidal cycles. Therefore the channel was divided along the middle and fish from each side were counted separately. The number of *A. anableps* counted every 15 min from each side was referenced to the respective transect length and averaged between the two sides (mean ± S.D.). The values are presented in the standardized form 'number of *A. anableps* per metre of channel bank' (number m^{-1} channel bank).

Simultaneously to a census, the water level was measured using a tidal gauge (±1 cm) in the main channel. The tidal current speed was determined by measuring the time it took the tidal current to stretch a 10 m long tape attached to a weight with a buoy using a stop watch.

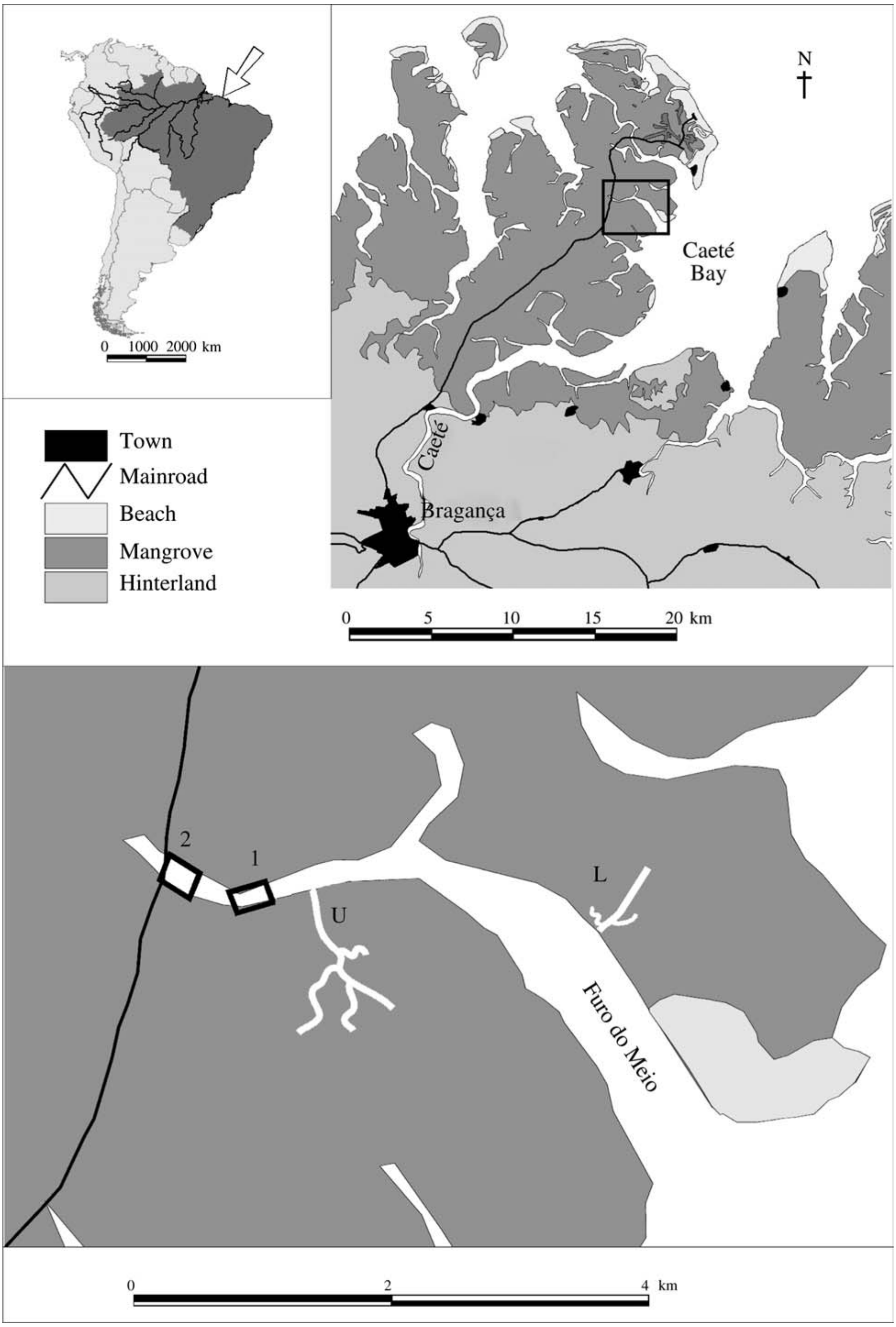

FIG. 1. Study area north of the city of Bragança (Pará, north Brazil) and sample sites along the main channel Furo do Meio in the centre of the mangrove peninsula. 1 and 2, two corridors for visual census of *Anableps anableps* in 2001 and 2002, respectively; U and L, two first order mangrove creeks in the upper and lower reaches of the Furo do Meio, respectively, used for block net studies in 2001.

CATCHES IN THE INTERTIDAL MANGROVE

In order to study temporal and spatial changes in feeding and abundance of *A. anableps*, two first order intertidal creeks were blocked at slack HW, one in the upper and the other in the lower reaches of the Furo do Meio (*c.* 2 km apart) (Fig. 1) between 16 March and 9 May 2001 (wet season). Salinities were generally low, increasing from 5 in March to 12 in May. Creek surveys at neap tides revealed that the upper creek (15 566 m^2) was approximately twice the size of the lower creek (7693 m^2) (Fig. 1).

During two consecutive lunar cycles, 32 block net samples were collected (30×3 m, 50 mm stretched mesh-size). The different moon and tide phases and day and night changes resulted in four treatment groups: spring tide-night, spring tide-day, neap tide-night and neap tide-day (SN, SD, NN and ND, respectively). The HW at SN, SD, NN and ND occurred at *c.* 1900, 0700, 0100 and 1300 hours local time, respectively. At each moon phase, four consecutive tidal cycles were sampled in the sequence 'upper creek at night, upper creek at daytime, lower creek at night, lower creek at daytime'. Fish were collected at LW. Most *A. anableps*, grouped in small puddles upstream of the net, were usually caught alive. At three strong spring tides, the sampling was interrupted to save the net. *Anableps anableps* already entangled in the net were collected but only used for stomach analysis. Altogether, 29 block net samples were used to compare abundances: in the upper creek three, three, four and four at SN, SD, NN and ND (sum: 14); and in the lower creek four, three, four and four at SN, SD, NN and ND (sum: 15), respectively.

Three-way ANOVA was used to test whether the number of *A. anableps* [$\log_{10}(x + 1)$-transformed to normalize the data] caught with the block net differed between creeks, tides and time of day. Differences in density (fish m^{-2}; square-root-transformed to normalize the data) at neap tides were compared for the factors creek and time of day using two-way ANOVA. Spring tide abundances were not standardized to density because at spring tides the entire mangrove plateau was flooded and the area inundated could not be determined.

LENGTH RELATIONSHIPS, CONDITION FACTOR AND SEX RATIO

In the field, sex, total length (L_T, cm) to last full cm and total wet mass (M, ±1 g) were determined. The L_T and M relationship for females and males was calculated using the equation $\log_{10} M = \log_{10} a + b \log_{10} L_T$. For each sex, the coefficients a and b were calculated by the method of least-squares regression. To verify if the calculated b was different from the isometric value ($b = 3$), a t-test (H_0: $b = 3$) was used. The slopes of the regression lines (females and males) were tested for homogeneity (Sokal & Rohlf, 1995). The condition factor K of females (*f*) and males (*m*) was calculated for each individual fish: $K = \left[\sum(100 M L_T^{-3}) n_{f,m}{}^{-1}\right]$ (Ricker, 1975; Cinco, 1982). A χ^2 test was used to test whether the observed sex ratio was equal to an expected ratio of 1:1.

Since the division between stomach and intestine in *A. anableps* is not discernible, the entire gastrointestinal tract (GIT) from the oesophagus to the anus was removed and conserved in 10% formalin. Also, the length of the uncoiled GIT of 56 specimens (22 males, 77–191 mm L_T; 34 females, 63–231 mm L_T) was measured (L_{GIT} ±1 mm). The relative length of the GIT (L_{RGIT}) for males and females was calculated: ($L_{RGIT} = L_{GIT} L_T^{-1}$). The feeding habit was classified according to Odum (1970) who suggested a L_{RGIT} of <1, 1–3 and >3 for carnivorous, omnivorous and herbivorous fishes, respectively. The fish were assigned to four size classes: 12–14, 15–17, 18–20 and >21 cm L_T.

STOMACH FULLNESS AND DIGESTION STAGE

In the laboratory, GITs were washed, drained on an absorbent paper and wet-weighed (±0·01 g). GITs were opened and GIT fullness was assigned to five categories according to Dalpado & Gjøsæter (1988): empty, filled to 30%, filled 30–70%, filled 70–100% and 100% full with a stretched GIT with thin walls. To ascertain whether the original GIT fullness index (I_{GIT}) differed by tide, time of day and creek, a three-factor ANOVA was calculated that, however, was invalid due to heteroscedasticity. Therefore, a three-factor ANOVA with bootstrapped *P*-values was calculated (Efron & Tibshirani, 1993). Resampling was carried out using observed S.D. within data cells and no homogeneity of variances was assumed. Bootstrapping was carried out by using data step capabilities of SAS.

The digestion stage of the entire GIT content was assigned to four categories according to Dalpado & Gjøsæter (1988): recently eaten, <30% digested, 30–70% digested and >70% digested. GIT fullness and digestion stage of all fish analysed were assigned to the eight groups that resulted from the combination of the factors creek, tide and time of day.

STOMACH CONTENT ANALYSIS

GIT contents were washed out onto a sieve (diameter 63 µm) and transferred to 50 ml Kautex bottles (4% formalin). Empty GITs were drained and wet-weighed. The mass of the GIT contents (M_{GITC}) was calculated as $M_{\mathrm{GITC}} = M_{\mathrm{GITF}} - \mathrm{M}_{\mathrm{GITE}}$, where M_{GITF} was the wet mass of the removed GIT (g) and M_{GITE} was the wet mass of the empty GIT (g). The I_{GIT} was calculated as $I_{\mathrm{GIT}} = 100\ M_{\mathrm{GITC}}\ M^{-1}$.

Contents were washed in distilled water to remove formaldehyde before contents were observed under a stereo magnifying glass and identified to the lowest possible taxon. Within Arthropoda, only Crustacea were identified to lower taxa. Araneae and Insecta were not further identifiable. Each taxon was briefly drained and then wet-weighed (±0·00001 g). Items <0·00001 g in mass were included as 0·00001 g. Whenever possible, fragments were assigned to the appropriate taxon and weighed together. Unidentifiable fragments were weighed separately and assigned as 'remains'.

The mud found in GITs was separated, dried (72 h at 60° C) and weighed (dry mass = M_{MD}). The samples were heated in a muffle furnace (5 h at 530° C) and weighed (ash free dry mass = M_{MAFD}). The difference between M_{MD} and M_{MAFD} gave the amount of organic carbon (g), which should have been available for an animal feeding on mud.

STANDARDIZATION OF MASSES OF FOOD ITEMS

The effect of fish size within the four different size classes was accounted for by standardizing GIT content masses to the geometrical mean mass of all investigated fish of one size class according to Brenner *et al.* (2001). A linear regression between *M* and M_{GITE} was established. Subsequently, mass ($M_{p_{j,i}}$) of each prey item *j* found in the GIT of a fish *i* of mass M_{i} was standardized ($M_{p_{j,i}\,s}$) using the geometrical mean mass (M_{GM}) for the size class to which the fish with the M_{i} belonged: $M_{p_{j,i}\,s} = M_{p_{j,i}}(a + bM_{\mathrm{GM}})(a + bM_i)^{-1}$. Using $y = 0{\cdot}0422x - 0{\cdot}1572$ ($r^2 = 0{\cdot}82$; $n = 255$), the original GIT content masses were converted into standardized GIT content masses (Brenner *et al.*, 2001).

FEEDING STRATEGY AND PATTERNS IN DIET COMPOSITION

The feeding strategy of *A. anableps* was assessed using the plot of Costello (1990). The prey-specific abundance was based on wet masses.

The similarities in diet composition between sample combination and size class were displayed using non-parametric multi-dimensional scaling (MDS) (Clarke & Warwick, 1994). In the original species-sample table, each cell contained the mean standardized mass of food item (g) per size class and factor combination (*e.g.* UNN1 = upper creek, neap tide-night, smallest size class). Square-root transformation was used to generate the Bray-Curtis similarity indices. 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), where a stress value between 0·1 and 0·2 still gives a potentially useful two-dimensional picture.

FOOD CONSUMPTION

The individual I_{GIT} values were sorted according to the factor combinations SD, SN, ND and NN, and average I_{GIT} for each group were calculated. The average I_{GIT} of the daytime and the nightly inundation were added up to provide a measure of the daily consumption in % body mass of *A. anableps* at spring and neap tide. This is not a conventional measure of evacuation rate. It was assumed that the stomach contents at the end of ebb tide were the minimum of what the fish had eaten and that the LW period was not a feeding period for *A. anableps*. Thus, the consumption calculated here is a conservative measurement.

RESULTS

MAIN CHANNEL CENSUSES

The censuses in the Furo do Meio main channel revealed a clear tide-related alternation in abundances of *A. anableps* with high abundances at LW and low abundances at HW irrespective of neap, mid or spring tide (Fig. 2).

As soon as the flood tide started, main channel abundances of *A. anableps* started to decrease. Within an hour after slack LW, *A. anableps* were almost completely absent from the main channel. Only very few *A. anableps* remained close to the main channel banks throughout the phase of inundation at daytime. The majority of *A. anableps* swam with the flood tide into the intertidal creeks where they foraged during inundation. With the falling tide *A. anableps* returned from the intertidal creeks, however, the abundances of *A. anableps* in the main channel started to increase again only after the ebb current speed maximum was over (Fig. 2, spring tide). *Anableps anableps* were in the mangrove *c.* 3 h at flood and 2 h at ebb tide, totalling *c.* 5 h per tide that *A. anableps* spent in the mangrove creeks (Fig. 2).

Maximum abundances occurred during the quasi-stagnant LW phase in the subtidal parts of the main channel. Considering the entire width of the main channel, mean ± S.E. abundance at slack LW at neap tides was 0·127 ± 0·003 *A. anableps* m^{-2}. Correlating the abundance to the corridor of 1 m width along each bank in which the distribution was concentrated, mean abundance was 1·91 ± 0·05 *A. anableps* m^{-2}. Sometimes large synchronized swimming schools were observed at LW in the main channel (170–370 individuals).

When related to water level, the pattern of decline in fish abundance at flood tide was congruent with that of the increase at ebb tide [Fig. 3(a)]. Only at the end of ebb tide (water level *c.* 0·5 m above mean LW) did the numbers surpass those at flood tide when many *A. anableps* left the mouths of the first order creeks to congregate at the main channel banks. In contrast, when related to time after HW, the migratory pattern was not congruent for flood and ebb tide, indicating that tidal migration of *A. anableps* at neap tides is controlled by water level and not by time [Fig. 3(b)]. Spring tides displayed the same pattern.

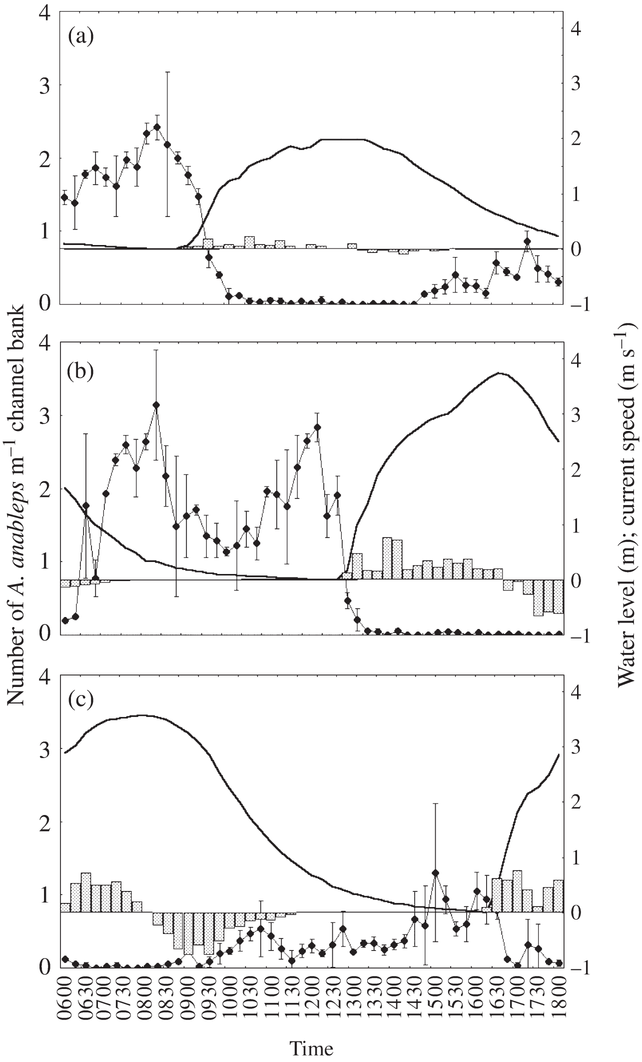

FIG. 2. Representative cycles of the mean ± s.e. number of *Anableps anableps* (●) ($n = 2$, left and right channel bank) per metre of bank (visual census) in the main channel of the Furo do Meio at (a) neap, (b) mid and (c) spring tide during daylight hours. —, water level for the main channel. Positive and negative current speeds (▨) correspond to flood and ebb tide, respectively.

INTERTIDAL ABUNDANCE

The number of *A. anableps* caught from the mangrove creeks was higher at daytime than at night (three-way ANOVA, $F_{1,20}$, $P < 0{\cdot}05$); creek and tide had no significant effect; and there were no interactions. Neap tide density of *A. anableps* was higher in the lower than in the upper creek and again higher at daytime than at night (two-way ANOVA, creek: $F_{1,12}$, $P < 0{\cdot}05$; time of day: $F_{1,20}$, $P < 0{\cdot}05$). Mean ± s.e. HW density was 0·0012 ± 0·0002 m^{-2}, thus being *c.* 100 times lower than the densities in the main channel at LW.

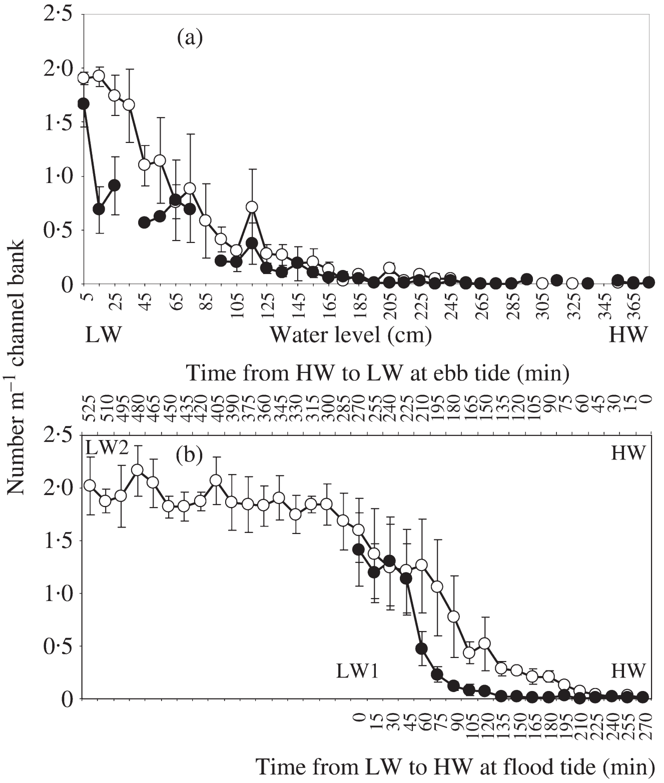

FIG. 3. (a) Mean ± S.D. number of *Anableps anableps* m^{-1} channel bank (visual census) in the main channel of the Furo do Meio at flood (●) and ebb tide (○) at increasing and decreasing water levels above mean low water, respectively ($n = 6$ neap tide cycles). LW, slack low water; HW, slack high water. (b) Mean ± S.D. number of *A. anableps* corresponding to the time from the first LW (LW1) to HW at flood tide (●) lasting a maximum 270 min (lower abscissa) and the time from HW to the next LW (LW2) at ebb tide (○) lasting a maximum 525 min (upper abscissa) ($n = 6$ neap tide cycles).

LENGTH RELATIONSHIPS, CONDITION FACTOR AND SEX RATIO

A total of 384 *A. anableps* were caught in the first order creeks. The L_T and M relationships of *A. anableps* are shown in Table I. The coefficient b was significantly <3, for females (t-test, d.f. $= 178$, $P < 0{\cdot}001$), males (t-test, d.f. $= 78$, $P < 0{\cdot}001$) and both sexes (t-test, d.f. $= 251$, $P < 0{\cdot}001$). The low b suggests that *A. anableps* increases more in L_T than predicted by its increase in M. For male *A. anableps*, b was low and the S.E. was high, probably due to the small size range covered.

The b values of females and males were not homogenous (test of equality of slopes, d.f. $= 248$, $P < 0{\cdot}05$). There was a clear sexual dimorphism in *A. anableps*, probably linked to vivipary: on average, females were larger (mixed size classes up to 17 cm L_T, whereas all size classes >18 cm consisted entirely of females), females were heavier at a given L_T, and increased faster in M than

TABLE I. Total length (L_T) and mass (M) relationships and gastrointestinal tract length (L_{GIT}) of male (M) and female (F) *Anableps anableps* from mangrove creeks near Bragança, Pará, north Brazil

Relationship	Sex	a	S.E. of a	b	S.E. of b	L_T range (cm)	n
L_T and M	F	0·0516	0·0745	2·5170	0·0597	12–25	173
L_T and M	M	0·1230	0·1796	2·1437	0·1543	12–18	79
L_T and M	F + M	0·0336	0·0635	2·6549	0·052	12–25	252[a]
L_T and L_{GIT}	F	1·1154	0·0951	1·2128	0·0792	7–23	34
L_T and L_{GIT}	M	2·3006	0·1608	0·9146	0·1331	8–19	22

[a] Out of 255 specimens used for stomach analysis, three individuals were left unsexed due to damage by *Callinectes* sp. *n*, sample size.

males (higher b in females). There was no significant difference between the K of females (mean ± S.D. 1·307 ± 0·208) and males (1·256 ± 0·190) in the wet season (two-sided t-test, d.f. = 250, $P > 0·05$).

The female:male relationship of 2·2:1·0 was significantly different from an expected 1:1 ratio (χ^2, d.f. = 23, $P < 0·05$). This does not necessarily reflect a heterogeneous sex relationship in the population, however, since smaller males could have passed through the mesh of the net used.

Anableps anableps had a long and thin GIT with weak musculature. The L_T and L_{GIT} relationships of female and male *A. anableps* are shown in Table I. The mean ± S.D. L_{RGIT} was 1·95 ± 0·30 ($n = 56$). The L_{RGIT} in females (2·03 ± 0·06) was significantly greater than in males (1·83 ± 0·05) (Kruskal–Wallis test, $n = 56$, $P < 0·05$).

STOMACH FULLNESS AND DIGESTION STAGE

The three-factor ANOVA showed that each main effect had a significant effect on I_{GIT} and that there was no interaction: GITs were fuller at spring tide than at neap tide, fuller at daytime than at night-time and fuller in the lower creek than in the upper creek (Table II).

The proportions of the GIT fullness stages and of the digestion stages at NN, ND, SN and SD in the upper and in the lower creek generally followed the same pattern (Figs 4 and 5). In the lower creek, where the pattern was clearest [Figs 4(b) and 5(b)], the proportion of the categories '100% and stretched' and '70–100% full' ascended in the sequence NN, ND, SN and SD. Likewise, the proportion of empty GITs descended in the sequence NN, ND, SN and SD. This pattern was reflected in the digestion stage [Fig. 5 (b)] where the proportions of the categories 'recently ingested' and '<30% digested' ascended in the sequence NN, ND, SN and SD. Hence, high GIT fullness correlated with the highest proportions of recently ingested food and *vice versa*. In the upper creek, fish consistently had less full GITs, and food was consistently more fully digested at NN, ND, SN and SD than in the lower creek (Figs 4 and 5). Both ascending (GIT fullness) and descending trends (digestion stage) from NN towards SD were less clear in the upper creek, most likely due to a low sample size of the SN group [Figs 4(a) and 5(a)].

TABLE II. A three-factor ANOVA with bootstrapped *P*-values of the gastrointestinal tract fullness index of *Anableps anableps* caught with block nets set at slack high tide, north Brazil. Factors: tide (neap and spring tide), time of day (day and night) and creek (upper and lower creek)

Source	d.f.	SS	*F*	*P*
Tide	1	201·13	9·7314	0·0010
Time of day	1	646·10	31·2612	<0·0005
Creek	1	288·43	13·9555	<0·0005
Tide × time of day	1	11·55	0·5589	0·4375
Tide × creek	1	0·13	0·0064	0·9055
Time of day × creek	1	11·93	0·5774	0·3460
Tide × time of day × creek	1	2·60	0·1257	0·6505
Error	247	5104·94		

CONSUMPTION

On average (±S.D.) the fish had eaten 5·1 ± 4·7% (range: 0·0–21·5%; $n = 255$) of their wet mass per tide. The food consumption of *A. anableps* at NN, ND, SN and SD is shown in Table III. Although site effects on I_{GIT} were detected (see above), consumption data from both creeks were pooled to provide a broader use of the values. At neap and spring tides, daytime consumption was 2·8 and 1·6 times higher than at night respectively. The mean daily consumption was 11·8 and 7·3% per body mass of *A. anableps* at spring and neap tides, respectively, or *c.* 1·6 times higher at spring tides. The overall mean daily consumption was 9·6% per body mass of *A. anableps*.

FOOD ANALYSIS

A total of 255 specimens was used for stomach analyses. *Anableps anableps* fed mainly on red macroalgae (foliaceous *Catanella* sp., filamentous *Bostrychia* sp.) that grows as a dense cover on the above ground root system of the mangrove trees around the mean HW level. Other important food items were Insecta, small crabs of the family Grapsidae (most of them probably *Goniopsis cruentata* Latreille) and at neap tides also mud. Less important diet components were Gammaridae, Polychaeta, Capitellidae, Araneae, Littorinidae and Mytellidae.

Anableps anableps subsisted primarily on *Catanella* sp., which was eaten by 62% of the fish, while its average contribution to the GIT mass was 55% (Fig. 6). Insecta was consumed by 63% of the fish, but only contributed to <2% of the GIT mass. The other prey taxa occurred in 22–50% of the GITs, but their average contribution to the GIT masses of the fish was low, indicating a generalized feeding strategy for these food items. *Anableps anableps* exhibited a high within-phenotype component where most of the individuals used many resource types simultaneously. Mud was clearly of minor importance in the feeding strategy of *A. anableps*. Although mud was the second most important food item in

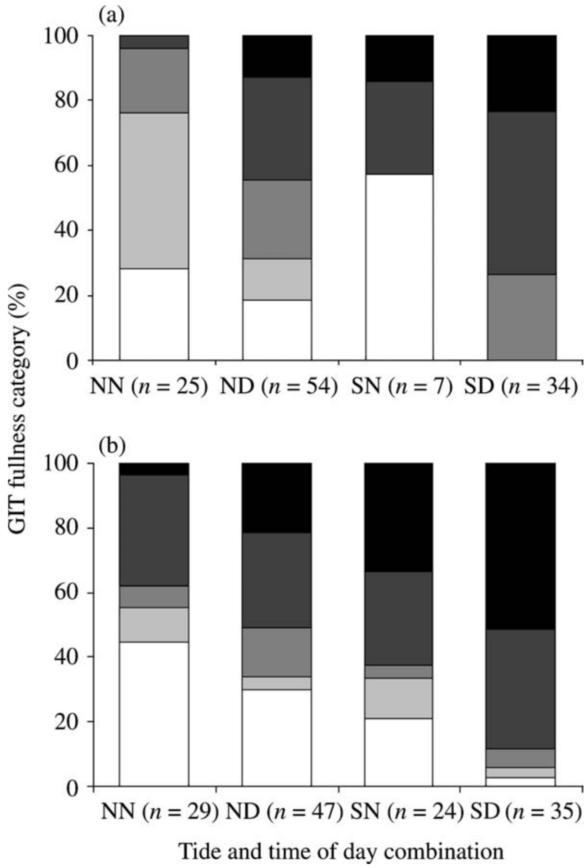

FIG. 4. Proportion of gastrointestinal tract (GIT) fullness categories of *Anableps anableps* (■ 100% stretched, ■ 70–100% filling, ■ 30–70% filling, ▨ <30% filling, □ empty) from two first order mangrove creeks of the Furo do Meio: (a) upper and (b) lower creek at neap tide-night (NN), neap tide-day (ND), spring tide-night (SN) and spring tide-day (SD). The number of GITs analysed (*n*) is given for each treatment combination. Fish were caught by blocking creeks at slack high water in the wet season 2001.

terms of mass, it was eaten by only 16% of the fish, which was by far the lowest value of occurrence found among all major food items.

CHANGES IN DIET COMPOSITION

In the lower creek all size classes, and hence both sexes, fed on the principal food items *Catanella* sp. and *Bostrychia* sp. at SD, SN, ND and NN [Fig. 7(e)–(h)]. The amount of food ingested during daylight inundations (SD, ND) was higher than during darkness (SN, NN), both at spring and neap tides. At spring tides *A. anableps* consumed more than at neap tides. The diet was more diverse; Insecta and Grapsidae were eaten in greater amounts, *e.g.* on average (both creeks) 23 Insecta per GIT in the size class 15–17 cm at SD. In the lower creek, mud occurred only at NN in the diet of the two smallest size classes. The GITs did not contain mud in any spring tide.

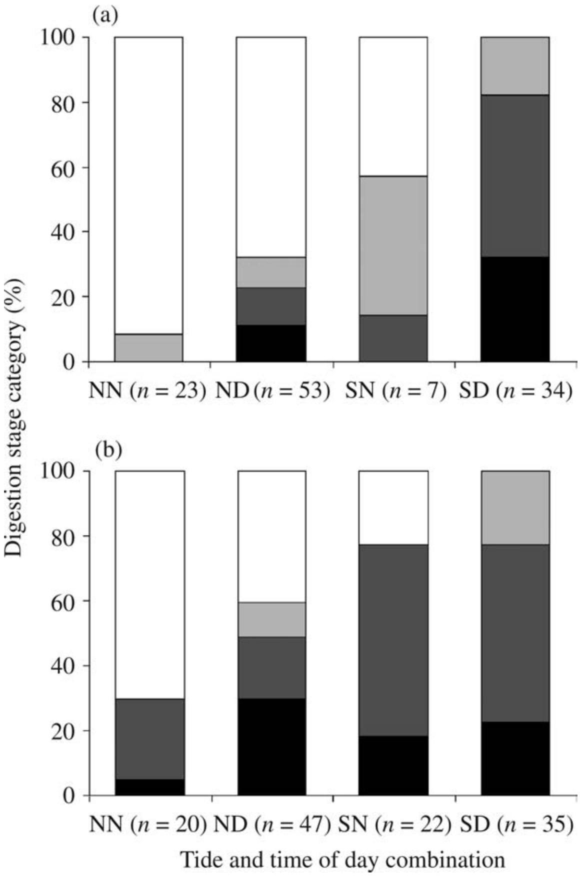

FIG. 5. Proportion of digestion stage categories of *Anableps anableps* (□ >70% digested, ░ 30–70% digested, ▓ <30% digested, ■ ingested recently) from two first order mangrove creeks of the Furo do Meio: (a) upper and (b) lower creek at neap tide-night (NN), neap tide-day (ND), spring tide-night (SN) and spring tide-day (SD). The number of GITs analysed (*n*) is given for each treatment combination. Fish were caught by blocking creeks at slack high water in the wet season 2001.

In the upper creek [Fig. 7(a)–(d)], fish caught at SN and NN had almost empty GITs [Fig. 7(b), (d)]. Therefore, the daylight inundations in the upper creek contrasted more clearly with nightly inundations than in the lower creek. Higher consumption in the spring tide in the upper creek was still apparent. As in the lower creek, mud was only consumed at neap tides, in this case both at ND and NN. The overall mean ± S.D. for both creeks of organic carbon in the mud ingested was 0·16 ± 0·13 g at ND and 0·07 ± 0·06 g at NN. Mud constituted on average (±S.D.) 12 ± 32% of the GIT wet mass in the specimens that had ingested mud ($n = 43$).

The cluster dendrogramme [Fig. 8 (a)] distinguishes four groups of diet compositions according to the combination of the factors creek, tide, time of day and L_T class, also indicated in the MDS plot in Fig. 8(b). Groups I, II and III consisted of almost empty GITs containing different food items in insignificant amounts. The majority (63%) of the factor combinations were arranged

TABLE III. Mean ± S.D. consumption of *Anableps anableps* per body mass (%*M*) per semi-diurnal tide and per day (daytime and night-time summed) at spring and neap tides. Fish were caught from first order intertidal mangrove creeks in north Brazil using a block net at slack high water from March–May 2001 (wet season)

Tide and time of day combination	Consumption tide^{-1} (%*M*)	*n*		Consumption day^{-1} (%*M*)
SD	7·2 ± 3·6	69	Spring tide	11·8
ND	5·4 ± 5·3	101		
SN	4·6 ± 4·7	31	Neap tide	7·3
NN	1·9 ± 2·7	54		

SD, spring tide-day; ND, neap tide-day; SN, spring tide-night; NN, neap tide-night; *n*, number of specimens in each group.

in group IV characterized by GITs containing considerable amounts of food. On closer examination, group IV showed two subgroups at 54% similarity (IVa and IVb). The subgroup IVa consisted of neap tide diets containing mud. The GITs in subgroup IVb contained considerable amounts of food except mud. Almost empty GITs were found in the upper creek only (groups I, II, III). Likewise, GITs containing mud were mainly found in the upper creek (group IVa). Poor diets were only encountered at neap tides, with poorest feeding success linked to the combination UNN (group I, II). Except for USN1 (group III), spring tide GITs were well filled. The L_T class, and hence the sex, had no effect on changes in diet composition. All fish caught (≥12 cm L_T) that had consumed considerable amounts of food had fed on the same diet.

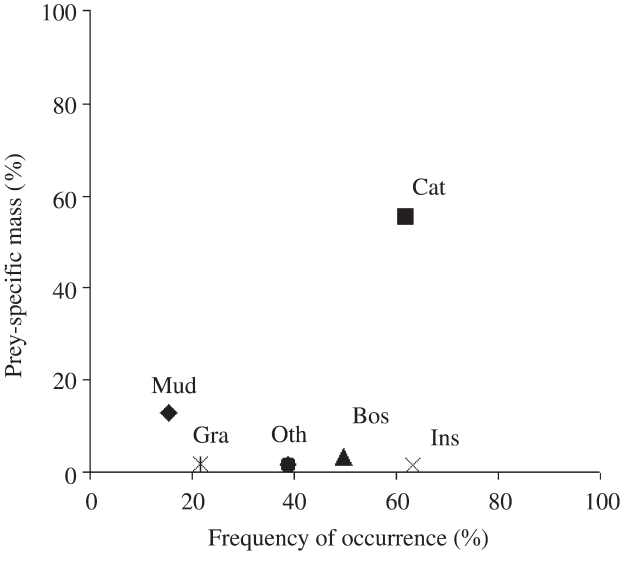

FIG. 6. Costello-plot of *Anbleps anableps* (*n* = 255) caught in the mangrove channel Furo do Meio in the wet season 2001. Cat, *Catanella* sp.; Gra, Grapsidae; Oth, others; Bos, *Bostrychia* sp.; Ins, Insecta.

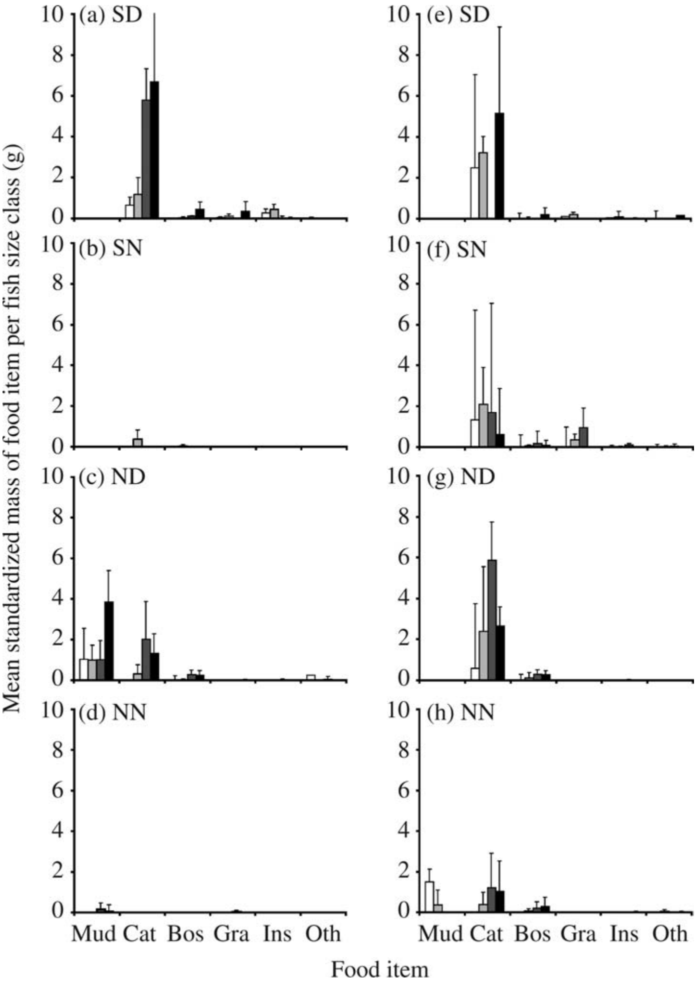

FIG. 7. Food composition of *Anableps anableps* (mean ± 95% CI wet mass) caught at different combinations of the factors tide and time of day [spring tide-day (SD), spring tide-night (SN), neap tide-day (ND) and neap tide-night (NN)] from two first order intertidal mangrove creeks (a)–(d) = upper creek and (e)–(h) = lower creek in the wet season 2001. The sample sizes according to the total length classes (☐ 12–14 cm, ▨ 15–17 cm, ▨ 18–20 cm, ■ >21 cm) were: (a) 14, 13, 4, 4; (b) 1, 5, 1, 0; (c) 10, 17, 12, 15; (d) 4, 10, 7, 3; (e) 17, 13, 0, 4; (f) 6, 14, 2, 2; (g) 6, 19, 13, 8; (h) 6, 10, 5, 9. Masses of food items were standardized per fish size class. Cat, *Catanella* sp.; Bos, *Bostrychia* sp.; Gra, Grapsidae; Ins, Insecta; Oth, others.

DISCUSSION

TIDAL MIGRATION

The macrotidal regime in the Amazon delta is likely to synchronize the tidal periodicity in both juveniles and adults of many fish species. The results from the Furo do Meio show that, for instance, the first flood rise was the trigger for not only the virtual disappearance of *A. anableps* from the main channel but

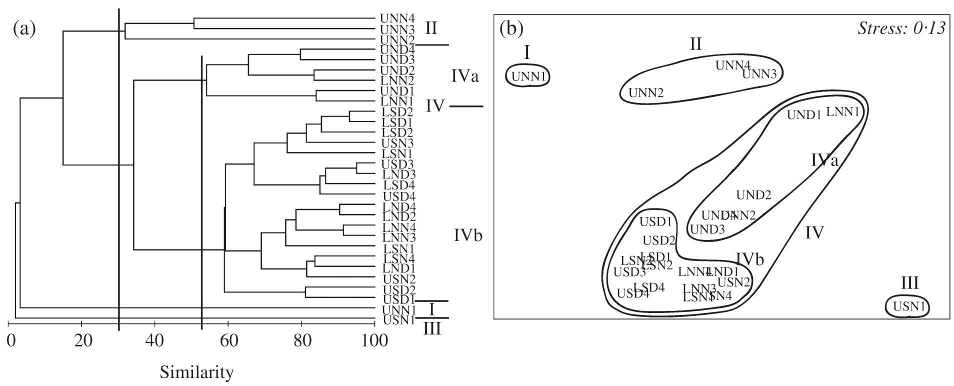

FIG. 8. Cluster dendrogramme (a) and multi-dimensional scaling plot (b) of the similarities in food composition of *Anableps anableps* caught in two first order mangrove creeks (U, upper creek; L, lower creek) of the Furo do Meio in the wet season 2001 at four tide-time of day combinations (SN, spring tide-night; SD, spring tide-day; NN, neap tide-night; ND, neap tide-day) and of four total length classes (1, 12–14 cm; 2, 15–17 cm; 3, 18–20 cm; 4, >21 cm). Groups in (a) and (b) were separated at similarity levels of 30% (—) and 54% (--).

immigration into the intertidal creeks. Shallow-water hydroacoustics revealed that the entire fish community, 'invisible' below the water surface, rides the tide each first flood rise to achieve upstream transport (Krumme & Saint-Paul, 2003; Krumme, 2004). Besides the synchronization of fish movement in response to favourable flood current phases, the occurrence of fishes in the intertidal mangrove zone is synchronized on a medium time scale by the spring tide and neap tide pulse (Krumme *et al.*, 2004). Diurnal patterns, however, clearly differ interspecifically (M. Brenner, U. Krumme & U. Saint-Paul, unpubl. data).

The tidal migration of *A. anableps* was triggered by the water level, not by the relative time after LW or HW, clearly suggesting that the sample design in tidal-related studies on fish species should be oriented according to equal flood and ebb water levels instead of equal times after LW or HW.

The early immigration into and late emigration from the intertidal creeks by *A. anableps* probably maximizes foraging time (Kneib & Wagner, 1994). Moreover, the fish maximize the time they gather close to the bank in very shallow water. The preference for this microhabitat may be linked to early access to the intertidal creeks with the lateral widening of the channel during first flood rise. This enables the fish to be the first to encounter the intertidal resources, for instance arthropods that have fallen onto the previously exposed grounds. It may also reduce both the risk of longitudinal displacement at higher current speeds and the risk of piscine predation from deeper waters. Lawrie *et al.* (1999) showed that *Neomysis integer* were concentrated in a band toward the moving tide edge to avoid areas of high flow.

Slack HW coincides with maximum Secchi disk readings in the tidal cycle. Hence, *A. anableps* always foraged during the periods of highest water clarity in the shallow mangrove creeks and encountered optimal visual conditions for underwater vision (food search, *e.g.* on aufwuchs). The smallest *A. anableps*, in particular, were often the first to literally ride on the tip of the flood tide into the intertidal creeks followed by the larger sizes. At spring tide HW the smallest *A. anableps* were often observed foraging on the mangrove plateau around *A. germinans* pneumatophores in very shallow water (<10 cm deep), suggesting an ontogenetic separation in habitat use. Likewise, in captivity the juveniles select the shallow-water zones to search for mosquito larvae (H. Greven, pers. comm.).

DIET COMPOSITION

Greven *et al.* (2002) describe that the mouth of *A. anableps* is terminal, orientated slightly downwards, and assumed that *A. anableps* ingests food from the bottom in shallow water. The clear specialization on intertidal, near-surface food resources, the phylogenetic development of the above-water eye, the poor diving capability (Greven *et al.*, 2002) and the obvious surface swimmer shape of *A. anableps*, however, render the suggestion of bottom-oriented feeding unlikely. *Anableps anableps* occupy the outermost niche on the coastal ecotone between aquatic and terrestrial habitat. The most important food items in the diet of *A. anableps* are usually found near the water surface. *Catanella* sp. co-occurring with *Bostrychia* sp., Littorinidae and Mytellidae are found only as part of the aufwuchs on the above ground mangrove root system. The vertical distribution of aufwuchs is restricted to a horizontal band of a few decimetres around the mean HW level.

Anableps anableps offers an interesting plant–animal interaction by removing epiphyte coverage from the aboveground mangrove root system, thus fulfilling a mutually beneficial cleaning function. The positive effect animal grazers have on growth and production of mangrove roots by removing associated aufwuchs was shown by Perry (1988), Wada & Wowor (1988, 1990) and suggested by Koch & Wolff (1996).

The elongated body of *A. anableps* is probably related to acceleration during jump attacks on above-water prey items such as Insecta. The fish have been observed foraging for drowned insects that have fallen from the canopy and skilfully attacking living prey (*e.g.* ants or Aranae) by jumps onto stilt roots in the forest around HW, similar to the behaviour observed by Wothke & Greven (1998).

Anableps anableps attack *Goniopsis cruentata* when these crabs climb down the stilt roots (to moisten their gills) during periods of inundation in the mangroves.

At LW adult *A. anableps* were observed feeding on fish carcasses and making jumps onto the mud to catch Insecta (S. Peterhaensel, pers. comm.).

The mean relative length of the GIT of *A. anableps* (1·95) points to an omnivorous feeding habit according to the classification of Odum (1970). Although the dominance of red algae in the diet suggests herbivorous feeding, *A. anableps*, in fact, has an omnivorous feeding habit. The average dry mass of red algae on the stilt roots did not exceed 1 g dry mass m^{-2} (D. Schories, unpubl. data). There was a significant difference between mass, number and thenutritional value of the food items found in the GITs of *A. anableps*. The GITs often contained only the empty, low-mass chitin carapaces of Insecta.

A calorimetrical estimate instead of a prey-specific mass for the food items would facilitate the understanding of the real importance of food items in a fish diet. Such an approach would probably change the interpretation of Fig. 6, where *A. anableps* seemed to exhibit a generalized feeding strategy with specialization on *Catanella* sp., to a more mixed feeding strategy with varying degrees of generalization and specialization on prey types such as Insecta and Grapsidae (Costello, 1990). Insecta probably represent an abundant and nutrient-rich food resource for many mangrove fishes (Robertson, 1988; Ley *et al.*, 1994; Krumme *et al.*, 2004).

Anableps anableps apparently relied entirely on intertidal prey, except when feeding on ubiquitous mud at neap tides. Zahl *et al.* (1977) and Greven *et al.* (2002) have suggested that *A. anableps* feed on the substratum and mud from the water edge. The results of this study suggest that mud is of minor importance in the diet. It can be assumed that the main food items eaten under the best conditions (at SD) are likely to be the preferred food items for a given species (in this case *Catanella* sp., Insecta, Grapsidae). Furthermore, mud is permanently available irrespective of time and water level, but was only taken up at neap tides. The sediment surface of the intertidal mangrove slopes, on average, contained 2·5% organic carbon per g sample wet mass (Koch, 1999), suggesting that mud was just an alternative food item consumed under restricted foraging conditions, and probably having only poor nutritive value for the fish. Due to its generalized feeding strategy, however, it seems *A. anableps* have developed considerable adaptive flexibility in coping with changes in the local food supply and availability.

TEMPORAL AND SPATIAL CHANGES IN FEEDING

It can be assumed that higher water levels provide a greater foraging habitat for fishes on intertidal coasts. The topography of the plateau mangrove of the Caeté estuary results in a *c.* 50% increase in inundated mangrove areas with a small change in water level increase above mean HW (Cohen *et al.*, 2000). Although on a yearly basis the plateau mangrove is rarely completely flooded (*c.* 3·3% of the time; U. Krumme, unpubl. data), inundation involves an extraordinary increase in the surface area and foraging habitat for *A. anableps*.

The results show that illumination was the most important factor determining the feeding success of *A. anableps* in intertidal mangrove creeks. Irrespective of spring or neap tides, daytime inundations were always linked to a higher intertidal abundance of *A. anableps*, greater I_{GIT}, and lower digestion stages than nightly inundations. This clearly emphasizes the importance of the above-water eye in the foraging of *A. anableps*. The digestion stage of the animal prey items in the GITs, however, did not allow species-specific determination, and hence the inference to their diel activity patterns. Consequently, it cannot be ruled out that diel changes in prey activity augmented foraging conditions for the better in daylight.

It can be concluded that the combination of the factors 'tide' and 'time of day' resulted in a positive interaction yielding the best foraging conditions at SD. The ND provided the second-best conditions although habitat accessibility was low. The interaction at SN, when habitat accessibility was high but darkness hampered visual foraging and there were fewer fish, foraging conditions ranked third. At NN, when low water levels coincided with darkness, the resulting interaction of the ambient factors was negative.

Additionally, the results highlight the importance of creek location. On average, I_{GIT} and abundance of *A. anableps* was higher and digestion stage was not as advanced as in the lower creek. In the upper creek, *A. anableps* foraging at SN and NN had almost empty GITs. These results do not allow for an absolute conclusive explanation for this spatial pattern, but it is fair to assume that factors such as creek size and topography, hydrography of the Furo do Meio drainage system, and spatial distribution of aufwuchs are involved to some extent.

The results show that the quantity of food consumed by *A. anableps* was clearly influenced by the factors tide, time of day and site, while the qualitative composition of the diet was not. In Fig. 8, all GITs with a common diet dominated by red algae are shown as distinct from the empty GITs and neap tide GITs containing mud.

ENERGY FLOW IN A PULSING SYSTEM

In the cycle of energy production in a mangrove ecosystem, intertidal fishes transfer energy from the eulittoral to the subtidal area, by the consumption of food and migration to their subtidal resting sites. The feeding and migration of an estuarine fish species such as *A. anableps* occur entirely within the mangrove environment, thereby energy is retained within the system. The results show that consumption by an intertidal fish can change with the tide and the light:dark cycle, as well as with site. The increased foraging area under spring tide conditions was linked to a higher consumption (*c.* 60%) and a greater feeding success of *A. anableps* than at neap tides. Spring tide conditions may not only foster the foraging success of *A. anableps*, but also that of other intertidal mangrove fishes, and most probably even of the entire intertidal fauna (Krumme & Liang, 2004). Higher inundations and stronger tidal currents at spring tides may intensify the coupling between intertidal and subtidal mangrove fauna and flora. Moreover, the overall exchange between mangrove estuary and its adjacent coastal area may be increased at spring tides.

Additionally, the diurnal cycle is of importance. Though food consumption of *A. anableps* was higher at daytime than at night-time, however, diurnal changes in food consumption probably are species-specific.

This has important implications for food web modelling in macrotidal mangrove areas. During the neap tide period, the interaction between system compartments in the Caeté mangrove estuary is relatively low (low inundation and current speeds) compared to the highly dynamic spring tide periods (high inundation and current speeds). The quasi-weekly alternating tidal pulse produced a system of two states, characterized by their different level of disturbance. Focussing on only one level of disturbance (*e.g.* only on spring tide, but not on neap tide) in a modelling approach may lead to significant misinterpretations of the overall system dynamics (Wolff *et al.*, 2000).

The authors are grateful to Chico, Ilson and A. Echterhoff for assistance and entertainment in the mangrove. S. Peterhaensel kindly provided data for the determination of the relative GIT length of *A. anableps*. We thank H. Greven, J. Leal-Flórez and S. Peterhaensel for revising this manuscript and the anonymous reviewers for their comments. W. Wosniok helped in applying bootstraps. This work resulted from the cooperation between the Center for Tropical Marine Ecology (ZMT), Bremen, Germany and the Univ. Federal do Pará (UFPa), Belém, Brazil, under the Governmental Agreement on Cooperation in the Field of Scientific Research and Technological Development between Germany and Brazil financed by the German Ministry for Education, Science, Research and Technology (BMBF) (Project number: 03F0253A, Mangrove Dynamics and Management - MADAM), and the Conselho Nacional de Pesquisa e Tecnologia (CNPq) (MADAM contribution 80).

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