

Intertidal migration of the four-eyed fish *Anableps anableps* in North Brazilian mangrove creeks

Uwe Krumme^{1,2,*}, Marianna Audfroid Calderón¹, Andreas Echterhoff¹

¹Leibniz Center for Tropical Marine Ecology (ZMT), Fahrenheitstr. 6, 28359 Bremen, Germany

²Thünen Institute of Baltic Sea Fisheries (TI-OF), Alter Hafen Süd 2, 18069 Rostock, Germany

ABSTRACT: The movement patterns of mangrove fish during tidal cycles are virtually unknown, yet needed to understand fish habitat use. The intertidal migration of the four-eyed fish *Anableps anableps* L. (Anablepidae, Cyprinodontiformes), a surface-swimming species, was observed along 2 large mangrove-lined creeks in North Brazil. The number, direction and size of the fish crossing fixed line transects were recorded at 5 min intervals using visual surveys during daylight at spring, mid- and neap tide cycles. Migration took place in a surge and was predictably structured and directly related to water level, current speed and direction, and recurred independent of creek and tide. The fish rode the early flood tide upstream towards the creek heads. After the ebb current peak, they returned in a surge along the same pathways. The intertidal distances travelled ranged from 0.7 to >2 km per tide. Fish density maxima occurred at early flood and late ebb tide, with more fish swimming alone during flood tide and largest group sizes during ebb tides. At neap high tides, fish aggregated in fewer accessible creek heads. When spring tides inundated wider creek areas and made additional creek heads available, maximum fish dispersal occurred. Small fish underwent migrations at shallower water depths than larger fish, thereby optimizing foraging and refuge time. Creek heads were prime feeding grounds, and intertidal creeks were the pathways connecting trophic flows of *A. anableps*, highlighting that in the management of mangrove ecosystems, complete drainage systems deserve protection. Striking similarities in tidal migrations of resident salt marsh species suggest that equal evolutionary pressures resulted in universal migratory strategies of estuarine resident taxa.

KEY WORDS: *Anableps anableps* · Intertidal fish migration · Movement patterns · Mangrove creek · Microhabitat use · Visual census · Bragança · Pará

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INTRODUCTION

Mangroves are widely considered important nursery sites for many nekton species. While it is clear that numerous species are regularly present in mangroves, often with great numbers of individuals, information is scarce on how exactly they use the mangrove microhabitats in time and space. Extensive knowledge is available on the movement patterns of intertidal fish in other intertidal habitats, such as sandy beaches (e.g. Tyler 1971, Gibson 1973,

1980, Ansell & Gibson 1990), mudflats (e.g. Raffaelli et al. 1990), salt marsh creeks (e.g. Kneib & Wagner 1994, Bretsch & Allen 2006a,b, Kimball & Able 2007a,b) and rocky shores (e.g. Rangeley & Kramer 1995, Castellanos-Galindo et al. 2010). However, patterns in intertidal fish movement vary between coastal habitats, even within the same region (Castellanos-Galindo et al. 2010, Castellanos-Galindo & Krumme 2013). For instance, fish movements are restricted to flooded waterways in systems with dendritic creek systems, whereas movements

are wide-ranging on less structured open shorelines. Complex creek systems, especially those with intertidal vegetation, provide more edge, vertical structure and a variety of microhabitats for nekton than open shorelines, which may be linked to specific adaptations in intertidal habitat use.

Knowledge about intertidal microhabitat use is crucial to be able to understand ecological connections, define meaningful sampling designs and provide robust interpretation of sampling data. Regarding mangroves, understanding the role of different microhabitats for fish is of paramount importance for conservation and zoning. For instance, aquaculture ponds often invade from the landward side, destroying the uppermost sections of the mangrove forests, with largely unknown consequences for intertidal animals (Lee 1999).

Most mangrove forests of the world are subject to substantial tidal effects and constitute only temporary habitats for nektonic organisms, being accessible only during times of inundation. In these tidally influenced mangroves, fish have to move between low-water resting sites (LWRS) and high-water feeding sites (HWFS) to avoid stranding, thereby connecting subtidal and intertidal habitats (Sheaves 2005, Krumme 2009).

Mangroves have often been treated as a uniform habitat unit, regardless of the structural heterogeneity inherent in the large intertidal forests and mangrove-lined creek networks that dominate extensive tidal coastal areas. Yet, different mangrove microhabitats exist (e.g. Koch & Wolff 2002, Kon et al. 2011) and likely have different functions for fish and invertebrate species, which may result in heterogeneous animal distributions in inundated mangroves. For instance, species and size groups of shrimps seemed to use specific microhabitats during high tide (Rönnbäck et al. 2002, Vance et al. 2002, Meager et al. 2003), moving considerable distances into the mangrove (Vance et al. 1996). In the Philippines, Rönnbäck et al. (1999) observed differences in microhabitat use of shrimps and fish, and found highest fish abundance and biomass in the most inland habitat of the mangrove. In a temperate Australian mangrove, distinct patterns of fish assemblage zonation and strong edge effects were found (Hindell & Jenkins 2005). Giarrizzo et al. (2010) revealed a size-structured intertidal migration of the banded puffer fish *Colomesus psittacus* and suggested that the structure was related to ontogenetic changes in feeding and to the vertical zonation of hard-shelled prey items in the North Brazilian mangrove.

These findings from intertidal mangroves have mainly been inferred from blocking or enclosing areas of different mangrove zones or strata. This, however, has rarely been completed at different times of the tide because netting techniques are unable to capture the spatio-temporal simultaneity and complexity inherent in the intertidal migrations of animals. Other approaches such as underwater video, hydroacoustic observations or hydroacoustic imaging (e.g. DIDSON) have been successfully applied to study fish movements in mangroves and salt marsh habitats (Krumme & Saint-Paul 2003, Ellis & Bell 2008, Frias-Torres & Luo 2009, Kimball & Able 2012), but only captured the temporal patterns at the specific sampling location and were unable to account for the larger-scale spatio-temporal simultaneity involved in intertidal fish movements. Moreover, in tidally influenced mangrove environments, these approaches usually have limited capabilities due to a combination of adverse characteristics, such as high turbidity, strong tidal currents, litter transport, complex creek and forest structure, and extreme shallowness.

In the present study, we used human observers to visually record the movements of the four-eyed fish *Anableps anableps* (Anablepidae, Cyprinodontiformes) moving at different tides in 2 large intertidal mangrove creeks in North Brazil. The species always swims at the water surface except for brief submersions when heavily disturbed (Zahl et al. 1977) and thus gives us a unique opportunity for complete visual observations capturing the spatio-temporal simultaneity inherent in fish migrations through intertidal vegetated creek systems. *A. anableps* is a viviparous, estuarine resident species that uses mangrove creeks throughout its life. Reproduction takes place year-round; therefore, females require a constant food supply (Brenner & Krumme 2007, Oliveira et al. 2011). The species is distributed from the Gulf of Paria (East Venezuela, Trinidad) (Cervigón et al. 1993, Wothke & Greven 1998) to the state of Parnaíba/Piauí in northern Brazil (U. Krumme pers. obs.).

Brenner & Krumme (2007) showed that *A. anableps* in North Brazil rest in the subtidal zone in a linear distribution along the banks of sheltered channels during the low-water period (LWRS). Virtually all fish disappeared into mangrove-lined intertidal creeks early in the flooding tide and returned to the subtidal with the late ebb tide, but the course of the intertidal migration, distribution and microhabitat use in the inundated mangrove (HWFS) remained unknown. Stomach content analysis showed that the major food sources of *A. anableps* were epiphytic macroalgae,

Insecta and Grapsidae (Brenner & Krumme 2007), while stable isotope analysis suggested that the green algae *Enteromorpha* is the main food source assimilated (Giarrizzo et al. 2011). Brenner & Krumme (2007) found consistently fuller stomachs in fish returning from a creek near the edge of the mangrove peninsula than from a creek closer to the middle section, and hypothesized that creek size and topography, hydrography and spatial distribution of aufwuchs were involved in this difference; but the ultimate reason for the spatial difference in foraging success remained unclear.

The overall study objective was to determine the intertidal migration patterns of *A. anableps* in complex mangrove drainage systems. The following hypotheses were addressed: (1) tidal migration differs between creeks (of different topographical height) and between neap, mid- and spring tides; (2) fish are distributed homogeneously during their intertidal migration; (3) there is no size-structured pattern in the tidal migration; (4) group sizes do not vary during the tidal migration at flood and ebb tide.

MATERIALS AND METHODS

Study area

The study area is located within the world's largest contiguous mangrove coast, dominated by *Rhizophora mangle*, *Avicennia germinans* and *Laguncularia racemosa* (Nascimento et al. 2013). The study was conducted in the dead-ending channel Furo do Meio, a tidal tributary of the Caeté Bay, situated north of Bragança (Pará, Brazil) (Fig. 1a,b). The Furo do Meio is approximately 4.5 km long, draining the central part of a 180 km² mangrove peninsula. The mangrove plateau is trenched by dendritic creek systems that channel the tidal flow into the mangrove forest. The creek systems fall dry each tide, except for a degree of seepage water from mangrove sediments in the thalwegs. The subtidal channel holds water permanently (Fig. 1c) and provides the LWRS of *Anableps anableps* (Brenner & Krumme 2007). The order of the creek systems is defined as follows: no order is assigned to the permanently inundated subtidal Furo section, intertidal creeks draining into the subtidal Furo section are first-order creeks, and creeks draining into first-order creeks are second-order creeks. The upper reaches of the Furo have approximately 12 larger first-order creeks, while the lower reaches have about 8, which are dispersed over a larger area (Fig. 1c).

The tide is semidiurnal and asymmetric; flood tide lasts 4 h and ebb tide lasts approximately 8 h. During the last 4 h, the ebb tide in the subtidal Furo is extremely weak with an almost negligible fall in the water level due to sand banks at the mouth of the Furo. The tidal range is 2 to 3 m at neap tides and 3 to >4 m at spring tides. Water temperatures range between 25 and 31°C. Salinity 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, as an index for water turbidity, ranges between <5 and 100 cm at neap tide and between <5 and 40 cm at spring tide (U. Krumme unpubl. data).

Study sites

Fish were counted in 2 dead-ending first-order creeks approximately 2 km apart, one in the upper and one in the lower reaches of the Furo do Meio (Fig. 1c–e). The creek areas upstream of the mouth section (i.e. upstream of Transect 1; Fig. 1d,e) were surveyed and 3D maps were generated using GIS. The GIS model was used to calculate the inundated surface area (m²) and volume (m³) at different intertidal water levels to describe inundation characteristics of the creeks. Fish abundance was converted to density (no. m⁻²) by dividing fish counts by the inundated surface area upstream of the creek mouth section.

Visual censuses

Fish movements were counted simultaneously in the 2 creeks on 6 days in the early dry season of 2005 (n = 12 tidal cycles). Two expeditions were carried out at spring tides (June 22 and 23), 2 at mid-tides (June 25 and 26) and 2 at neap tides (June 28 and 29), thus covering the full range of inundation levels during a typical fortnightly cycle. Observations started at sunrise or with the start of the flood tide, and were restricted to daylight hours (06:00–18:00 h) because *A. anableps* escape from flashlights, and daytime inundations are the major feeding periods of the fish (Brenner & Krumme 2007). Observations at the second mid-tide and the 2 neap tides covered whole tidal cycles during daylight hours. However, the tidal and light cycles are not in phase. Consequently, observations at the 2 spring tides and the first mid-tide were split into one part in the morning (late flood tide and ebb tide) and one part in the evening (early

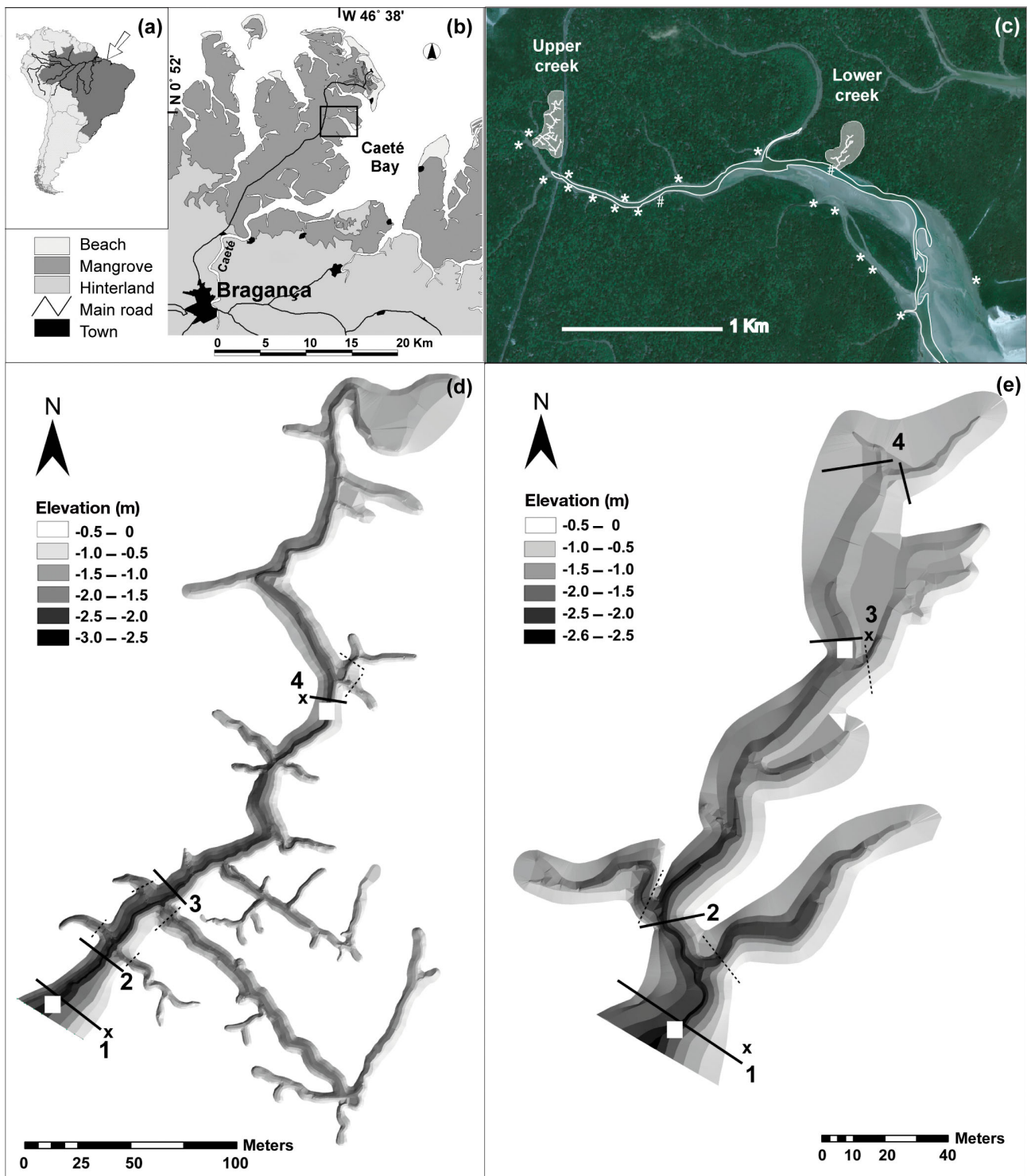


Fig. 1. (a) Study area in North Brazil. (b) Mangrove peninsula north of Bragança and Furo do Meio (frame). (c) Location of upper and lower creeks in the Furo do Meio with approximate drainage areas; subtidal area is outlined in white (satellite image taken at low water); *: first-order creek; #: first-order creeks sampled by Brenner & Krumme (2007). (d) 3D model of the upper mangrove creek and (e) lower mangrove creek; note different scales in (d) and (e). Numbers at continuous lines: location of line transects across the thalweg. Dashed lines: line transects across second-order creek. x: position of cameras. White square: location of tidal gauge

flood tide) because low-tide slack took place before sunrise and before sunset.

To record the temporal and spatial variation in fish movement inside the mangrove, line transects were placed at several observation points along each creek (Fig. 1d,e). A line transect was an imaginary line crossing a creek perpendicular to the tidal flow. Four permanent line transects were established in each creek (Fig. 1d,e). The number of fish that traversed the transect line in the up- or downstream direction during 5 min intervals was recorded. When fish crisscrossed the transect line, the net direction after 5 min was noted. Additionally, in the lower creek, fish were assigned into 2 size groups, small (approx. 4–8 cm total length [TL]) and large (>8 cm TL), to see whether different sizes moved at different times or water levels. Watches of all observers were synchronized to the correct local time. Each observer was assigned to a permanent line transect and remained still and quiet during the censuses. The fish passed mainly in the center of the creek several meters distance from the observer, so there is no reason to assume that fish behavior was significantly affected by the presence of the observers. Observers at the wider creek mouth transects had binoculars (10 × 40 Optolyth) to observe fish across the creek, which had a width of approximately 25 m at high tide. Other observers counted 1 transect across the first-order creek and monitored an additional 1 or 2 transects of nearby second-order creeks (e.g. Fig. 1d, Transect 3 plus the 2 adjacent transects).

It is important to mention that most observers were untrained. Therefore, there are some shortcomings in the quality of the census data that limited the accuracy of the analysis. Some observers switched from counting individuals during low-passage periods to adding estimated group sizes during high-passage periods. Some observers were unable to count the fish in second-order creeks sporadically or during flood or ebb tide because the movements in the first-order creek demanded their full attention. Therefore, despite a methodology of multiple observers, spatial patterns within creeks could not be analyzed in detail, particularly concerning the data from second-order creeks.

Water levels were measured every 5 min with a tidal gauge at Transects 1 and 4 in the upper creek and at Transects 1 and 3 in the lower creek (Fig. 1d,e). Likewise, current direction was noted and the surface current speed was estimated by measuring the time it took floating objects such as leaves to be transported between 2 wooden sticks set parallel to the current axis at known distances (2.5 and 5.0 m).

Additional tidal gauges were set in the subtidal channel of the Furo near the mouths of the first-order creeks to determine (1) the topographic height of the thalweg of the first transects above the low-water (LW) slack level (for the GIS model), (2) time delay between LW slack in the Furo and at the creek mouths, and (3) time delay in LW slack between the lower and upper creek (see Table 1).

Four camcorders were installed (upper creek: at Transects 1 and 4, lower creek: Transects 1 and 3) (Fig. 1d,e), each attached to a tripod and powered by a 12 V car battery. The camcorder records were used to determine current speeds for sample intervals with missing *in situ* measurements. The videotapes from the upper creek (Transect 4) and lower creek (Transect 3) were used to determine the group sizes of passing *A. anableps*. Fish were regarded as swimming alone when they were >0.5 m apart from the next fish. Group sizes were determined for fish that swam closer than 0.5 m to the next conspecific.

Data analysis

The sum of all fish that passed the mouth of a creek during ebb tide was used as an estimate of the total number of fish that had entered the creek during a given tidal cycle. This accounted for the fact that at spring tides, only the ebb tide was completed during daylight hours and enabled the inclusion of spring tides into the analysis. The assumption that fish that had entered at spring flood tides used the same pathway at ebb tide and did not 'disappear' into adjacent drainage systems is supported by (1) both creeks being dead ends, and (2) *A. anableps* displaying strong site fidelity to first-order creeks (M. Audfried Calderón unpubl. data). A 2-way ANOVA was used to test whether fish abundance (log [$x+1$]-transformed) differed between creeks (lower and upper creek) and tides (spring, mid-, and neap tide). The Kolmogorov-Smirnov test (KS test; normal distribution) and the Cochran test (homoscedasticity) were used to analyze whether the ANOVA assumptions were fulfilled. When a significant difference was detected (ANOVA $p < 0.05$), Tukey's multiple comparison test was used to identify individual group differences. Variables that did not meet the assumptions were tested using the non-parametric Kruskal-Wallis test (KW test) with the Nemenyi test for post hoc comparisons.

To track changes in fish density during the tidal cycles, the instantaneous number of fish present in a creek was divided by the inundated surface area for each 5 min interval. The inundated surface area was

Table 1. Some physical characteristics of 2 mangrove creeks used for visual censuses of *Anableps anableps* in the Furo do Meio, north of Bragança, Pará, Brazil. LWRS: low-water resting sites; δ LW: time delay of low-water slack

Parameter	Upper creek	Lower creek
Drainage area	~4.9 ha	~3.6 ha
Length of 1 st -order creek along thalweg	430 m	270 m
No. of larger 2 nd -order creeks	1	0
No. of smaller 2 nd -order creeks	14	5
Width of creek mouth	25 m	25 m
Slope (along thalweg)	0.23°, flatter	0.42°, steeper
Relative topographic height	Reference height	~0.5 m lower
Distance from creek mouth to LWRS	~300 m	~20 m
Duration (\pm SD) that creek is inundated at mouth (n = 4)	6 h 32 min \pm 30 min	7 h 49 min \pm 17 min
δ LW Furo and creek mouth	10–30 min	2–20 min
δ LW creek mouths	~15–30 min later	Reference time

derived from its relationship with the intertidal water level based on the GIS model. For each tidal cycle, the fish density estimates of 1 h before and after high-water (HW) slack (n = 25) were used to test whether HW fish densities differed between creeks and among tides (KW test).

The flooding periods and heights of the tidal cycles in the upper and lower creek were determined to assess differences in landscape settings. In addition, the time duration of 4 activity periods of the fish during a tidal cycle of 12 h 25 min were estimated: (a) flood tide immigration (the time in which n > 2 upstream fish were seen in successive 5 min intervals at Transect 1 at flood tide), (b) HW foraging (the time between the end of the flood immigration and the start of the ebb emigration), (c) ebb tide emigration (the time in which n > 2 downstream fish were seen in successive 5 min intervals at Transect 1 at ebb tide), and (d) resting in the subtidal channel during LW, i.e. $d = 12 \text{ h } 25 \text{ min} - a - b - c$. One-way ANOVA was used to test whether the time windows differed between creeks.

The frequency distribution of group sizes (data from the camera videotapes) was analyzed for flood and ebb cycles. The KS test was used to test whether, for a given creek, the frequency distribution of group sizes (pooled over all tides) differed between flood and ebb tide. The KS test was also used to test whether the frequency distribution of water levels at which smaller and larger fish from the lower creek were seen at Transect 3 differed between the 2 size groups at flood and ebb tide (pooled over all tides).

The linear distances traveled each tide between the observed feeding sites in the creek heads and the known resting sites in the subtidal section of the Furo were estimated for each creek based on the creek maps and the geo-referenced satellite image in Fig. 1c.

A 2 \times 2 contingency table was used to test whether the proportion of fish that swam beyond the uppermost Transect 4 and those that entered but did not swim beyond the uppermost transect differed between spring and neap tides. This was tested separately for each creek using the sum of the downstream fish at ebb tide from Transects 1 and 4.

RESULTS

Creek attributes

The 2 creeks differed in several aspects. The lower creek had an open *Rhizophora* forest with tree heights of 20 to 25 m, while the upper creek was dominated by a dense *Rhizophora* prop root coppice between 15 and 20 m. The lower creek was situated at a lower topographic level, was smaller and shorter, and had a steeper slope than the upper creek (Table 1). As a result, the lower creek was characterized by having on average (\pm SD) 0.51 \pm 0.16 m higher levels of intertidal inundation during the HW period, longer inundation periods (>1 h) and slower maximum current speeds at flood tide (Table 2). In addition, the mouth of the lower creek was located adjacent to the LWRS of the fish, whereas the mouth of the upper creek was located approximately 300 m upstream of the tip of the subtidal Furo area (Fig. 1c).

Despite these differences, the inundation properties for the elevations covered in the GIS model were analogous (Fig. 2). In both creeks, area and volume increased slowly with increasing intertidal water level until the latter reached approximately 2.6 m above the bed at the creek's mouth. Beyond 2.6 m, the water dispersed out of the creek network and the mangrove plateau became inundated. Values of creek area and volume increased above average. A

Table 2. Hydrological parameters June 22–29, 2005 in the upper and lower creek, measured at the creek mouth. n.m.: not measured

	Upper creek				Lower creek			
	Tidal range at creek mouth (m)	Max. flood current speed (cm s ⁻¹)	Max. ebb current speed (cm s ⁻¹)	Duration of inundation	Tidal range at creek mouth (m)	Max. flood current speed (cm s ⁻¹)	Max. ebb current speed (cm s ⁻¹)	Duration of inundation
Spring tide								
22 Jun	2.97	29	77	n.m.	3.27	14	52	n.m.
23 Jun	2.94	33	83	n.m.	3.25	17	75	n.m.
Mid-tide								
25 Jun	2.53	22	83	n.m.	3.12	n.m.	89	n.m.
26 Jun	2.54	22	54	7 h 15 min	3.15	13	71	8 h 5 min
Neap tide								
28 Jun	2.04	18	16	6 h 30 min	2.7	14	16	7 h 40 min
29 Jun	2.01	19	8	6 h 10 min	2.62	12	6	8 h

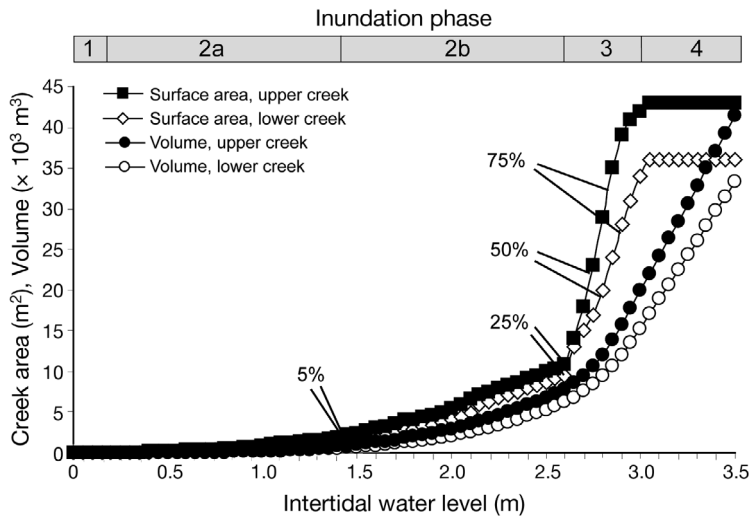


Fig. 2. Relationship between level of intertidal inundation and GIS-generated surface area (m²) and volume (×10³ m³) in the upper and lower creek. Five inundation phases (referring to creek mouth) are: 1: seepage water; 2a: inundation restricted to creek network, 5% of total inundated creek area (water level: 0.1 to ~1.5 m); 2b: inundation restricted to creek network, 25% (~1.5 to 2.5 m); 3: inundation leaving creek network and mangrove becoming inundated (26–99%) (~2.5 to 3 m); 4: mangrove plateau completely inundated (100%) (>3 m)

small water level increase of 15 cm caused a large upsurge of about 50% in the respective creek area and volume estimates.

Fish abundance and density among creeks and tides

The mean (±SD) number of fish that entered a creek per tide was significantly higher in the upper creek (256 ± 58) than in the lower creek (129 ± 42)

(2-way ANOVA, $p < 0.0001$). Fish abundance at neap tides was significantly higher than at spring tides, on average by 1.5 times (2-way ANOVA, $p < 0.02$). There was no significant interaction between creeks and tides ($p > 0.18$). As a consequence, fish densities in the upper creek were greater than in the lower creek (KW test, $\chi^2 = 142.4$, $df = 1$, $p < 0.0001$); in both creeks, fish densities were higher at neap tide than at spring and mid-tide (upper creek: KW test, $\chi^2 = 75.1$, $df = 2$, $p < 0.0001$; Nemenyi test, $p < 0.01$; lower creek: KW test, $\chi^2 = 41.2$, $df = 2$, $p < 0.0001$; Nemenyi test, $p < 0.01$).

Intertidal movement pattern

Our results revealed a consistent migratory pattern, which took place in tight response to changes in water level and current speed, and was unaffected by creek or tide (Fig. 3) (rejecting Hypothesis 1). The intertidal migration took place in a surge-like manner, i.e. the fish rode the early flood tide along the thalweg in water depths of 20–100 cm towards the creek heads, including the heads of first- and second-order creeks. Thereby, virtually all fish passed a given transect within 30–60 min. In response to short-term changes in current speed, the flood surge took place in phases of compressed passage across transects (unidirectional currents; many individuals crossing during a 5 min interval) and phases of extended passage (stagnant or even reversing current, especially at

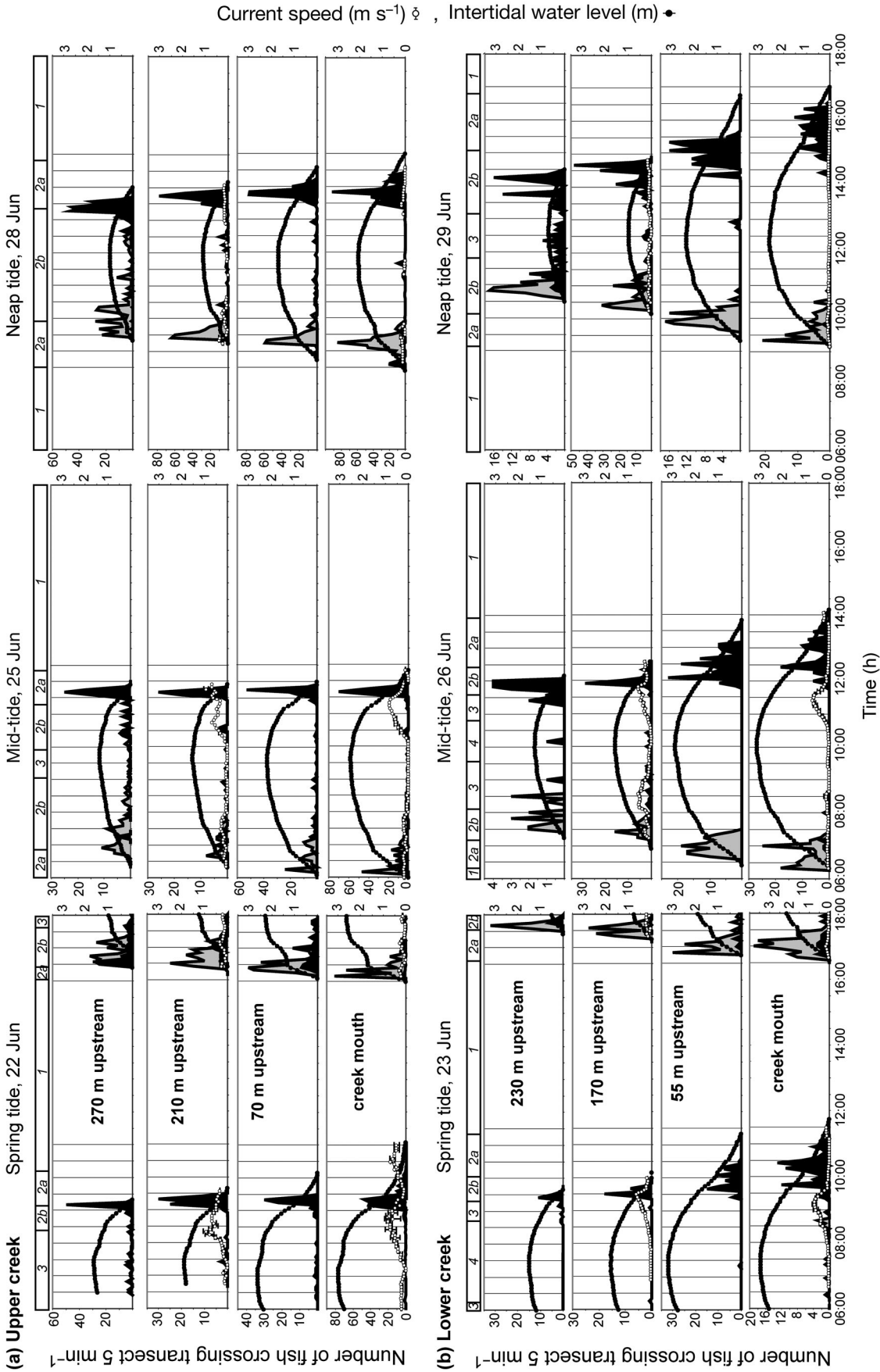


Fig. 3. Intertidal migration of the surface-swimming *Anableps anableps* along (a) upper and (b) lower creeks during spring, mid- and neap tides (22–29 June 2005). Simultaneous daylight visual censuses (sum of 5 min counts) on 4 transects of increasing distance upstream from the creek mouths (bottom to top; see Fig. 1 for transect locations). Shortened and lower inundations of upstream transects reflect higher topographic level. Grey area: upstream fish; black area: downstream fish. Filled circles: local water level. Open circles: current speed \pm 1 SE (measured at creek mouths and at upstream transect). Note different y-axes. Inundation phases on top of each panel refer to water levels at creek mouth transects (see Fig. 2 for inundation phase characteristics)

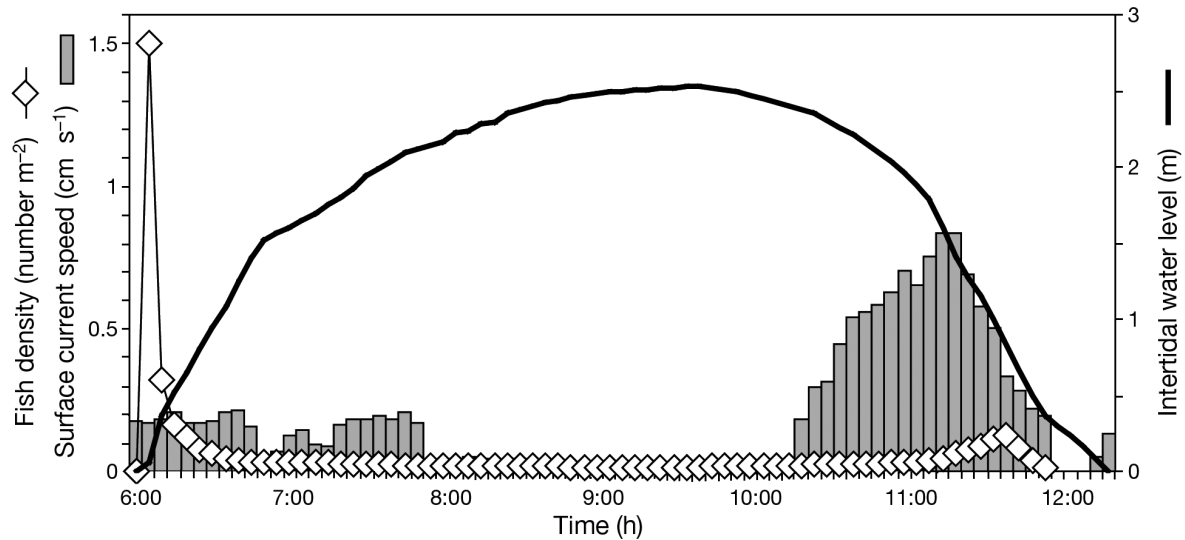


Fig. 4. Five-minute changes in water level, current speed and *Anableps anableps* fish density (fish m^{-2} , i.e. instantaneous total number of fish and inundated surface area upstream of the creek mouth) in an intertidal mangrove creek during a mid-tide cycle

neap tides, when it took 10–15 min for the fish to cross the next transect). During the HW period, almost no fish crossed the transects, as they were foraging in the creek heads, chasing and jumping for Grapsidae and insects on *Rhizophora* stilt roots or grazing on epiphytic algae from above-ground roots. At ebb tide, the fish returned along the same pathways in a surge but at water depths of 140 to 40 cm. Fish emigration only began after the maximum ebb current speed phase, being particularly evident at spring and mid-tides (Fig. 3; see video clip S1 in the Supplement at www.int-res.com/articles/suppl/m509p271_supp/).

The majority of the fish passed the transects swimming in the direction of the tide. On average, 10% were seen swimming temporarily against the tide. Once the fish entered a first-order creek in the early flood tide, they rarely returned. Consequently, each tide temporarily sub-grouped the fish and, as a result, foraging took place in distinct creeks before the fish re-merged in the subtidal channel during the LW period.

Fish density peaks

Generally, fish density peaked at flood start and late ebb tide (Fig. 4). The fish density peak at flood start (range: 0.2–15 fish m^{-2}) was usually 1 order of magnitude higher than the peak at ebb tide (range: 0.03–0.19 fish m^{-2}) and 2 orders of magnitude higher than throughout the remaining tidal cycle (range: 0.01–0.06 fish m^{-2}) (rejecting Hypothesis 2).

Size-specific movement pattern

A clear size-specific pattern in the intertidal migration of *A. anableps* was observed in both creeks, although it was only possible to collect data underpinning the size-specific pattern in the lower creek. At flood tide, the small fish entered the creeks in very shallow water before larger conspecifics, crossing the transects a few minutes earlier. At ebb tide, small fish returned a few minutes later than larger fish. Hence, small fish entered and left the creeks at slightly but significantly lower water levels than larger fish (rejecting Hypothesis 3; Fig. 5; KS tests, flood tide and ebb tide: $p < 0.001$).

Group sizes

Unlike the linear distribution along the banks during the LW period, >75% of the fish swam alone, in pairs or in groups of 3 during the intertidal migration (Fig. 6). At flood and ebb tide, most fish swam alone. However, at flood tide, almost 50% entered alone, and the maximum group size rarely exceeded 8 individuals. At ebb tide, only 25% left alone and significantly more individuals swam in groups both in the upper and lower creek (KS tests, upper and lower creek: $p < 0.001$). Group sizes of 5 to 12 were more abundant at ebb than at flood tide. Group sizes larger than 14 (maximum: 34 individuals) occurred exclusively during ebb tide (rejecting Hypothesis 4). For instance, large cohesive groups could be tracked

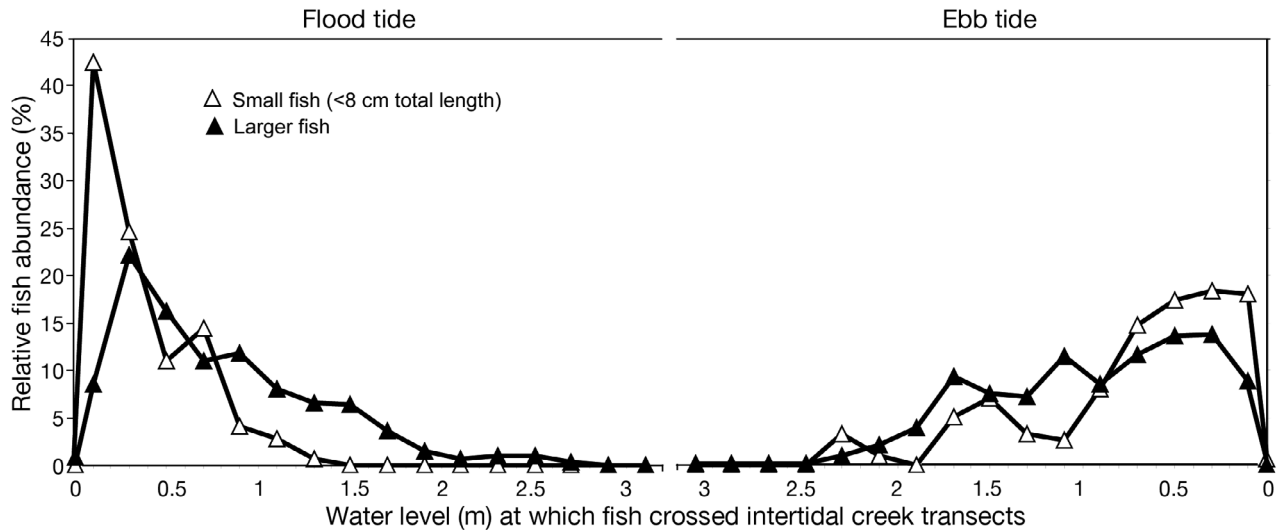


Fig. 5. Size-structured intertidal migration of *Anableps anableps* in North Brazil. Water levels (mid-points of 0.2 m classes) at which fish crossed intertidal transects in the lower mangrove creek. Relative fish abundance: proportion of fish during 6 flood tides ($n = 292$ small or < 8 cm total length, $n = 2756$ large) and 6 ebb tides ($n = 298$ small, $n = 2181$ large). Flood and ebb tide totals are unequal because spring flood tides coincided with twilight and therefore restricted daylight censuses

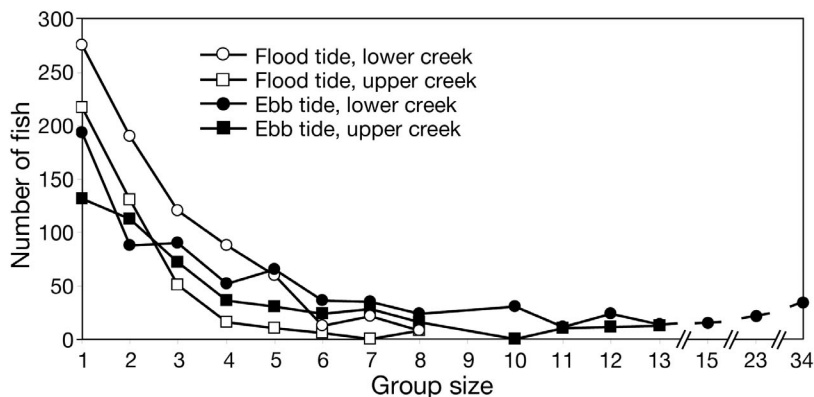


Fig. 6. Total number of *Anableps anableps* swimming alone (1 fish) or associated with others (2–34 fish) during 6 flood and 6 ebb tides across Transect 4 in the upper creek (flood: $n = 774$, ebb: $n = 733$), and Transect 3 in the lower creek (flood: $n = 438$, ebb: $n = 482$). Flood and ebb tide totals are unequal because spring flood tides coincided with twilight and restricted daylight censuses. See Fig. 1 for transect locations

from the uppermost transect downstream to the mouth of a creek at mid-ebb tide (Fig. 2a). The small *Anableps anableps* swam alone, in pairs or in groups of as many as 6 individuals.

Fish distribution during spring and neap tide

On average, 48% of the fish that entered a creek at flood tide swam beyond the uppermost first-order creek transect to forage in the creek head (range: 26–79%; data not shown). At neap tides, however, the portion of fish that swam beyond the uppermost transects was higher than at spring tides in both creeks

(2×2 table, upper creek: $\chi^2 = 205.1$, $p < 0.0001$; lower creek: $\chi^2 = 20.9$, $p < 0.0001$). Unfortunately, the spatial resolution of the censuses was not high enough to assess how fish abundances in the second-order creeks changed between spring and neap tides.

Migration phases

The fish stayed in the intertidal creeks on average (\pm SD) $89 \pm 4\%$ ($n = 8$ tidal cycles) of the time the creeks were flooded. Despite differences in the inundation periods between the creeks (Table 1), the time budgets *a*, *b*, *c* and *d* did not differ between creeks (1-way ANOVA, $p > 0.1$). On average (\pm SD), the fish were engaged with flood immigration for 90 ± 22 min, HW foraging for 193 ± 45 min, ebb emigration for 78 ± 36 min and resting in the subtidal channel for 364 ± 36 min (Fig. 7). The 4 migration phases therefore occupied 12, 26, 11 and 49% of the time, respectively, of a standard semidiurnal tide of 12 h 25 min.

Intertidal home range

A conservative linear estimate of the intertidal distance covered by *A. anableps* during 1 tidal migration (round-trip starting and ending at the subtidal site

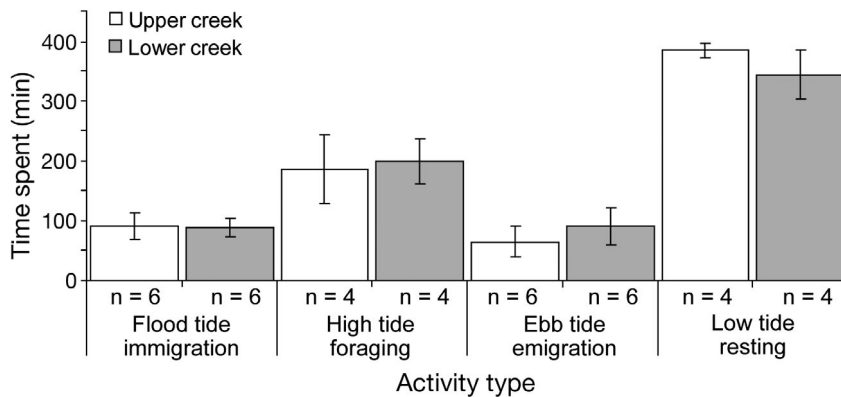


Fig. 7. Mean time duration (± 2 SE) of 4 major activity types displayed by *Anableps anableps* during a semidiurnal tidal cycle in the upper and lower creek. n: number of tidal cycles

closest to the mouth of a first-order creek) was 0.7 km for the lower creek and 1.5 km for the upper creek (Fig. 1c–e). However, given that first-order creeks can be longer than 1 km, in other instances the tidal migration may cover >2 km. The fish could thus travel >4 km during 2 tidal cycles, i.e. 1 lunar day. Assuming an average creek drainage system of 1 km length and 0.1 km width gives an estimated minimum intertidal home range of *A. anableps* of 0.1 km^2 .

DISCUSSION

The intertidal migration of *Anableps anableps* was non-random, predictably structured and closely synchronized with changes in water level and current speed. The overall pattern of the migration recurred each tidal cycle, regardless of creek location, tidal amplitude (spring, mid- or neap tide) and the time of semidiurnal HW (flooding at day or nighttime). *A. anableps* displayed persistent and straightened-out movements covering several hundred meters each flood and ebb tide, linked to a temporary inhibition of station-keeping responses, so that the movements can be considered a 'migration' following the definition of Dingle (1996). Opportunistic food intake, which occurred along the migratory pathway, only led to quick station-keeping responses, and the fish always continued swimming towards their HWFS or LWRS.

This study provides the first comprehensive picture of the spatio-temporal dynamics in intertidal migration and habitat use of an estuarine resident fish species from the large tidal drainage systems in North Brazilian mangroves (Fig. 8; see video clip S1 in the Supplement). During the stagnant LW period, *A. anableps* aggregated in shallow water along the banks

of the subtidal channel (Brenner & Krumme 2007). Shortly after LW slack, fish distribution along the subtidal banks dispersed and shifted into concentrations of fish at nearby first-order creek entrances. The fish then rode the early flood tide towards the heads of the drainage system within less than 2 h after LW slack. The late flood and early ebb phase comprised the foraging period in the creek heads (>3 h per tidal cycle), where the fish grazed on epiphytic algae and hunted for Grapsidae and insects on *Rhizophora* prop roots (Brenner & Krumme 2007). After the maximum

ebb current speed, the fish returned in a surge along the same pathways and associated with conspecifics from other first-order creeks along the subtidal banks during the next LW period.

Thereby, *A. anableps* repeatedly connected the furthest foraging sites in the creek heads of the mangrove forest with the resting sites in the shallow subtidal channel. This continuous movement thus transferred mangrove production to the subtidal by concentrating energy, protein and nutrients as body mass (Stevens et al. 2006). As natural mortality is assumed to be very low (vivipary) and their excretions are dispersed into the intertidal with the next tide, *A. anableps* likely function as an energetic loop that contributes to retaining production in the mangrove system. The important contribution of tidally migrating nekton organisms to the recycling of nutrients in marsh systems has been previously shown in the literature (Kneib 2000, Weinstein & Litvin 2000, Guest & Connolly 2004, Allen et al. 2013).

A comparison of the tidal migration patterns of *A. anableps* with available information on the banded puffer *Colomesus psittacus* (Krumme et al. 2007, Giarrizzo et al. 2010, U. Krumme unpubl. data), another important estuarine resident fish species from the same mangrove ecosystem, supports the concept that the use of mangroves by fish depends on species, size-class and microhabitat type. In both species, the intertidal migration was size-structured, i.e. juveniles entered earlier and returned later and thus maximized the duration of stay in the intertidal zone. However, in *A. anableps*, the time delay between size classes was narrower (a few minutes) compared to that of *C. psittacus* (approx. 1 h between small and large size class). Also, *A. anableps* migrated at lower water levels (0.2–1.4 m) than *C. psittacus*, and the tidal movements of *C. psittacus* were more protracted

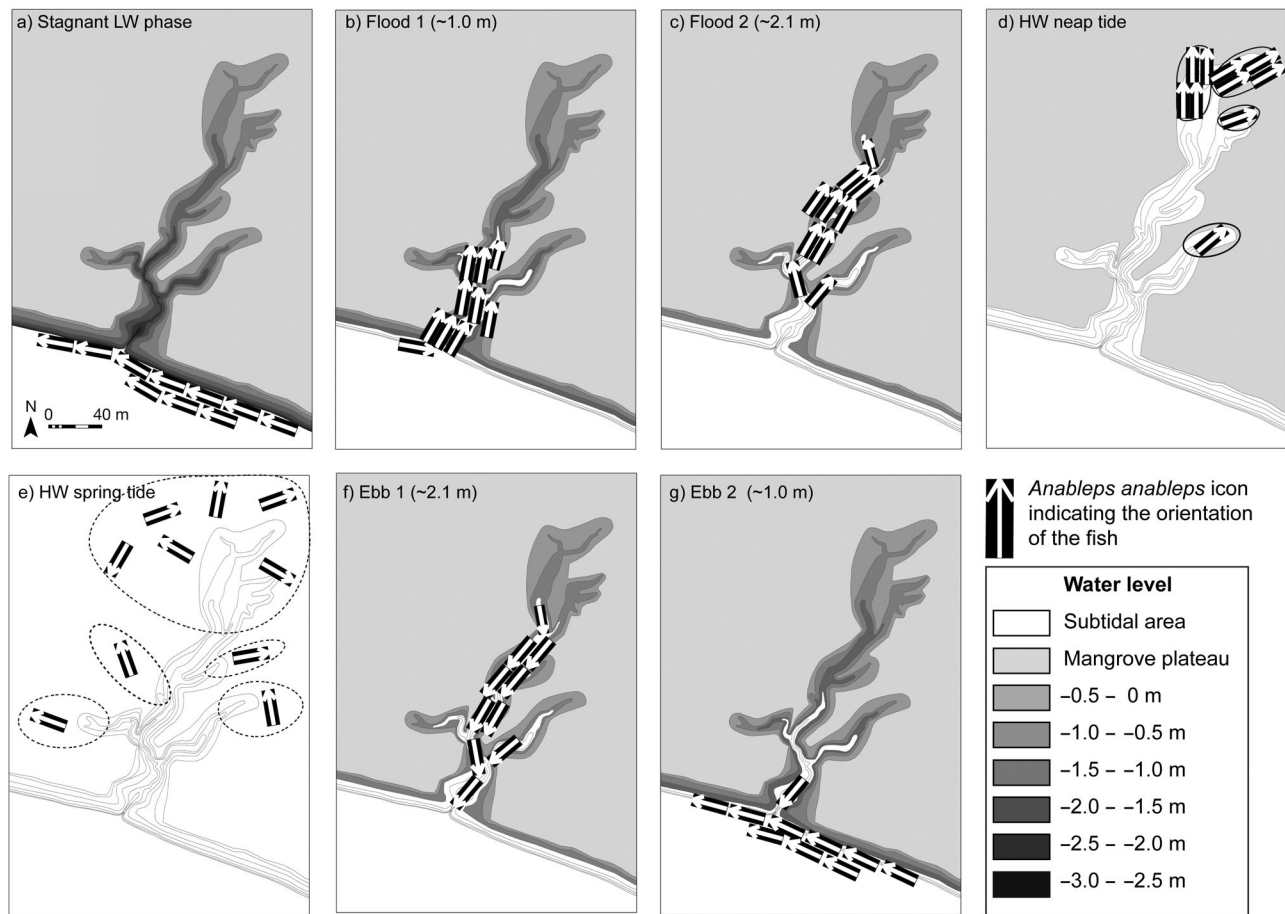


Fig. 8. Spatial distribution of water (white area) and *Anableps anableps* (icons) at different inundation levels in a macrotidal mangrove creek: (a) stagnant low-water (LW) phase, (b) flood tide of ~1.0 m, (c) flood tide of ~2.1 m, (d) high-water (HW) neap tide, (e) HW spring tide, (f) ebb tide of ~2.1 m, (g) ebb tide of ~1.0 m. Water levels refer to tidal height above the stagnant LW phase. Ten fish icons per panel indicate relative fish positions in a creek. Note different orientation of fish icons in panels; also note different fish distributions between (b) and (g), and between (c) and (f) despite equal water levels. Continuous line outlines in (d): distinct HW feeding sites at neap tides; dashed line outlines in (e): diffuse HW feeding sites at spring tides; see video clip S1 in the Supplement for details on *A. anableps* hunting grapsid crabs during spring tide HW

and did not take place in a surge but over a wider range of water levels (approx. 1–3 m). All size classes of *A. anableps* exploited a specific microhabitat (highest eu littoral zone of creek heads), whereas *C. psittacus*, foraging was more widespread, both horizontally and vertically, displaying a size-specific exploitation of different vertical mangrove zones (juveniles in the lower and adults in the higher eu littoral zone). This suggests that inter- and intraspecific differences in the timing of the intertidal migration and fish distribution during the inundation period are linked to the exploitation of different food resources whose access and availability is switched on and off by the tides, in interaction with the diel cycle.

Striking similarities exist between the tidal migrations of *A. anableps* and estuarine resident species from salt marsh creeks. First, resident nekton species

inhabiting US and European salt marshes are also known to aggregate at low tide in shallow subtidal areas located adjacent to the marsh and migrate to the vegetated intertidal as it becomes inundated, e.g. *Fundulus heteroclitus* (Fundulidae) (Kneib 1997) or *Pomatoschistus microps* (Gobiidae) (Hampel & Cattrijsse 2004). Second, resident taxa entered on the early rising tide and returned during late ebb tide stages (e.g. Cattrijsse et al. 1994, Bretsch & Allen 2006a, Kimball & Able 2012). Third, the tidal migration was structured, as resident taxa migrated at approximately the same depths at flood and ebb tide (Gibson 1973); however, modifications in water depths occur in response to biotic (Bretsch & Allen 2006b) and abiotic factors (i.e. creek drainage characteristics and current speeds in *A. anableps*). Fourth, feeding in the intertidal zone during high

tide is a major function of the tidal migration as it links HWFS with LWRS, fulfilling an important role in estuarine nutrient cycling. These remarkable similarities in the tidal migrations of resident taxa in tropical, subtropical and temperate vegetated, creek-dominated, estuarine environments throughout the Atlantic Ocean suggest that estuarine residents fulfill similar ecological roles in their systems. Moreover, similarities in the tidal migrations of resident taxa may result from equal evolutionary pressures towards optimization of intertidal habitat use, which resulted in the development of a universal intertidal migratory strategy. This strategy, as a result, benefited the survival of the species regardless of latitude, intertidal vegetation type and local tidal regime. Future comparative studies may further explore to what extent extrapolations of ecologically equivalent processes and functions of estuarine resident taxa between vegetated tidal environments (i.e. salt marshes and mangrove systems) are valid.

Functions of the tidal migration

The tidal migration of *A. anableps* fulfilled 3 important functions that are beneficial in this environment: (1) maximization of the foraging time in the intertidal; (2) reduction in energy use during transport by riding the tide; and (3) reduction in the risk of predation.

Foraging time maximization

The important role intertidal creeks play for *A. anableps* is evident as the species spent 90% of the time inside the creeks when flooded (approx. 6 h per tidal cycle). At flood tide, the fish could have hardly entered the mangrove creeks earlier, and at ebb tide, later return would have increased the risk of stranding. However, unlike in some salt marsh fish (e.g. Hampel & Cattrijsse 2004, Kimball & Able 2012), the intertidal densities of *A. anableps* were not equal between flood and ebb tide. The unbalanced fish density peaks were due to fish concentrating at the tip of the very early flood tide (see video clip S1 in the Supplement) when the inundated intertidal area was still very small (large numerator, small denominator). During the ebb tide return, slightly higher ebb tide water levels led to a larger inundated area and hence smaller density estimates. Small *A. anableps* displayed the optimized migratory strategy by spending more time inside the creeks than larger specimens.

At flood tide, small fish were the first ones able to collect invertebrates inundated by the tide or washed down by seepage water (U. Krumme pers. obs.), thereby using a spatio-temporal niche that likely decreased intraspecific competition for easily caught, high-quality food resources.

Reduction in energy use

Riding the flood tide was an apparent measure to conserve energy, being closely linked to the inundation characteristics of the tidal creeks. The fish entered slowly during neap tides and rapidly during spring tides, thus saving energy during movement towards the feeding grounds. The fish used temporary stays in mini-bays in very shallow water or in back-current areas to avoid being transported away from the entrance of a first-order creek at flood tide or being displaced downstream at ebb tide. As the fish returned to the subtidal with the last fall in water level, they ensured return to the LWRS with minor swimming efforts. The benefit of this behavior was further tested using small styrofoam buoys. Buoys set adrift prior to the ebb current maximum were transported out of the first-order creek while buoys set adrift together with the fish were transported downstream and usually stranded in the lower section or the mouth of the first-order creek.

Reduction in the risk of predation

Intertidal migrations of fish and shrimps may occur in response to changes in the risk of predation (Bretsch & Allen 2006b). This has been suggested in the nocturnal upshore migration of the plaice *Pleuronectes platessa* (Gibson et al. 1998) and the flounder *Platichthys flesus*, which migrated during nighttime because avian predators were less active at this time (Raffaelli et al. 1990). Innumerable hours of observation did not witness a single case of successful attack by birds or piscivores in *A. anableps*, suggesting that the principal function of the intertidal migration is feeding. However, the linear LW distribution of *A. anableps* along the unshaded permanent channel banks in very shallow water may be linked to a pay-off between avoidance of piscine predation in deeper waters and potential attacks from the mud banks and from the air (e.g. kingfishers and herons at daytime, fishing bats at nighttime).

The intertidal migration was characterized by a completely different fish distribution; the fish swam

mostly alone, in pairs or in groups of 3, differing in group size proportions between flood and ebb tide. A remarkable feature of the flood tide immigration was the resemblance between the above-water eyes of *A. anableps* and floating surface bubbles created by the air released from inundating crab holes. It is not known if this optical resemblance is mimesis and provides visual camouflage against potential predators in the shaded intertidal habitat when the fish enter at high densities in very shallow water. The human eye can distinguish *A. anableps* from air bubbles given the lined-up appearance, different trajectories and variable size of the latter. If it were mimesis, the exclusive occurrence of air bubbles at flood tide—and their lack during ebb tide—could partially explain the more dispersed fish distribution during the flood tide immigration. Alternatively, more individualized swimming during the upstream surge could ensure sufficient maneuverability in the tidal current, as suggested by occasional jumps and burst-and-coast swimming to avoid obstacles such as branches or roots in shallow water. The hunger state at flood tide may also favor more scattered swimming, while the state of satiation after feeding during ebb-tide (Brenner & Krumme 2007) may initiate the association with conspecifics in anticipation of the agglomeration during the LW period.

Spring–neap tide differences in fish distribution

Our results revealed that at neap tides, more *A. anableps* entered the creeks than at spring tides. At spring tides, the intertidal habitat accessibility was greater due to higher inundation levels, and thus the fish dispersed over more intertidal creeks (including small first-order creeks). At neap tides, less intertidal creeks were accessible, and the intertidal fish distribution was concentrated in fewer creeks (Fig. 8). Apparently, rising HW levels gradually recruited additional creek heads so that at spring tides, HWFS increased in number and size, resulting in maximum fish dispersal in the intertidal.

Spring–neap tide-related changes in fish distribution were also apparent at a lower spatial level, i.e. within the first-order creeks. At neap tides, dozens of fish were observed foraging at the tip of the tide in the heads of first-order creeks (see video clip S1 in the Supplement), suggesting that the preferred foraging areas in the creek heads were shifted downstream due to lower inundation levels. At spring tides, in contrast, overall, less fish arrived at the head of the first-order creeks, suggesting that a greater

proportion of fish foraged more downstream of the upper transect given the greater habitat accessibility due to higher inundation levels.

Intertidal home range

The movements of *A. anableps* were essentially 2-dimensional and mirrored the maximum extension of the tide on the horizontal and vertical plane. Unlike the distances travelled each tide in our study area (0.7 to >2 km), the tidal migration of *A. anableps* in microtidal Trinidad (tidal range: approx. 1 m) basically followed the up- and down-shore movement along the water's edge (Wothke & Greven 1998), hardly exceeding 100 m (H. Greven, University of Düsseldorf, pers. comm.) due to the absence of extensive drainage systems. Consequently, the distances covered by a species during tidal migrations may differ by >1 order of magnitude in response to different tidal regimes and environmental settings.

The size of the intertidal home range of *A. anableps* was similar to that of estuarine resident fish species from salt marshes. The intertidal home range of *F. heteroclitus* was 0.15 km² (Teo & Able 2003), and for the white perch *Morone americana* it was 0.11 km² (McGrath & Herbert 2009). This suggests that the minimum spatial requirement for the protection of estuarine resident fish species is the conservation of entire estuarine drainage systems. Smaller conservation units would fragment the home range of the fish.

Creek location affecting foraging conditions

Brenner & Krumme (2007) found fuller intestinal tracts in *A. anableps* from the lower creek compared to another creek from the upper reaches of the Furo do Meio. Our observations suggest that this was due to (1) greater habitat accessibility and (2) less competition for food in the lower creek. Greater habitat accessibility was caused by on average 0.51 m higher water levels during the HW period in the lower creek and is ultimately related to the relative creek location. Intertidal creeks of the lower reaches of the Furo (i.e. at the edge of the mangrove peninsula) have a steeper slope along their thalwegs, and the mangrove plateau is located on a lower topographic level relative to those in the upper reaches of the Furo, i.e. at the middle of the mangrove peninsula (Cohen et al. 2000, 2004). Likewise, better foraging condition in the lower creek could be due to overall

lower fish abundance, i.e. lower intraspecific competition, related to a lower number of first-order creeks and HWFS present in the lower reaches than in the upper reaches of the Furo do Meio. However, our sampling design could not separate the interactive effect of lower fish abundance and greater inundation levels in the lower creek. It is of note that slower growth of *F. heteroclitus* in complex salt marsh creeks was attributed to spatial variation in estuarine landscape structure (Kneib 2009). Webb & Kneib (2002) found a positive relationship between intertidal channel complexity and abundance of juvenile penaeid shrimps in a US salt marsh. Allen et al. (2007) found higher abundance of *F. heteroclitus* in salt marsh creeks with longer inundation times and higher inundation levels. Higher abundance and biomass of the pinfish *Lagodon rhomboides* and juvenile spot *Leiostomus xanthurus* were strongly related to creek depth, location, steepness and current flow (in order of importance; Allen et al. 2007). Despite disparities between our findings and those from salt marsh habitats, the results highlight that important links exist between creek location, estuarine landscape structure and accessibility of resources sustaining nekton production in vegetated intertidal environments.

Sampling in vegetated tidal environments

The sampling of mobile aquatic organisms in vegetated tidal environments usually requires the use of different gear types to account for a variety of habitat types, which automatically constrains the between-site comparison of samples. Moreover, comparisons among samples taken at different times during tidal cycles suffer from constant changes in water depth, current speed and flow direction (Kneib 1997). Spatially explicit sampling that considers the temporal variability in the distribution of mobile organisms is required to better understand the habitat use patterns of fish in complex environments (Kneib 1991, Rozas 1992). At present, there is no single method to capture the spatio-temporal simultaneity in tidal migrations of fish in turbid estuaries. In mangroves, the complex above-ground root system further exacerbates sampling. The use of hydroacoustics and underwater video can account for temporal variation by continuous observations but usually only provides point counts, and some practical limitations in turbid vegetated intertidal environments are discussed in Krumme & Saint-Paul (2003), Ellis & Bell (2008) and Kimball & Able (2012). Simultaneous visual surveys

of the surface-swimming *A. anableps* provided a unique opportunity to account for unprecedented detail for the spatio-temporal simultaneity inherent in the intertidal migration of an estuarine resident mangrove fish without sampling-gear bias. We are aware that the use of our methodological approach is likely restricted to the four-eyed fish. Simultaneous sampling at multiple transects along the migratory pathways of *A. anableps* (1) highlighted the spatial and temporal patterns in intertidal fish distribution that block net samples would have integrated into a single value; (2) identified the creek heads as the key microhabitat used for intertidal feeding (HWFS); and (3) thus provided important management recommendations, namely that the conversion of creek heads into aquaculture ponds would remove the major foraging grounds of *A. anableps* and disrupt the related trophic flows. Therefore, in the management of mangrove ecosystems, complete drainage systems deserve protection. Our results further demonstrate that flood and ebb tides are dynamic periods when nektonic communities are reshuffled; thus, point samples taken during these time intervals likely increase variation among the catches, which can lead to unwanted bias. Hence, to reduce variability and ensure comparability, samples collected in macrotidal environments should be taken before LW slack and around HW slack when assemblage compositions are most stable.

CONCLUSIONS

In the present study, we identified 3 important mangrove habitat units exploited by *A. anableps*: (1) the shallow water areas of the subtidal channel which hold the entire population during LW (LWRS), (2) the heads of intertidal creeks, which are the main feeding areas (HWFS) and (3) the intertidal creeks used as migratory pathways connecting LWRS and HWFS. The intertidal migration of *A. anableps* greatly resembled the migration of estuarine resident fish species from salt marsh habitats. Striking similarities in the tidal migrations of resident taxa (regardless of latitude, intertidal vegetation type and local tidal regime of the vegetated, creek-dominated, estuarine environments) may result from equal evolutionary pressures towards optimization of intertidal habitat use which resulted in the development of a universal intertidal migratory strategy, benefiting the survival of the species. Intertidal microhabitat use by fish can be very ephemeral in time and space due to the tidal dynamics. The remarkable changes in the (abun-

dance and density) distribution of *A. anableps* during the tidal cycles in this macrotidal mangrove accentuated the importance of the intertidal creek heads as essential HWFS. In times of proceeding loss of wetlands worldwide, the intertidal migration of *A. anableps* may serve as an excellent example for the claim that entire drainage systems have to be protected to ensure proper ecosystem functioning. The alteration of creek heads would remove the major foraging grounds of this estuarine resident fish species and disrupt related trophic flows. The dynamic and heterogeneous character of macrotidal mangroves, with an alternating mosaic of microhabitats, remains largely unrecognizable to us. Information on the individual level is needed to further understand microhabitat use by resident taxa in vegetated estuaries (e.g. Webb & Kneib 2002, Kneib 2009) and provide science-based recommendations to managers of vegetated tidal environments such as mangroves and salt marshes.

Acknowledgements. Our cordial thanks to the students from the Bragança Campus that participated in the *tralhoto* censuses: A. Silva, Adriana, Andreia, Carla, Cleidson, C. S. Costa, D. Simith, Diego, Erikson, J. Pantoya, João, Josiane, Lanna, E. Loopes, Marcelo, Márcio, M. S. Neves, Natalia, Rosa, S. Mara, Viviane, Wellington and Yrlano. We are grateful to T. S. Hoffmeister for discussions on sampling design and to W. Wosniok for statistical advice (University of Bremen). S. Schwantz (University of Bremen), A. Feyen, and C. Winkelmann helped in creating the 3D GIS model of the creeks, and A. Schubbauer analyzed video tapes. This work resulted from cooperation between the Center for Tropical Marine Ecology (ZMT), Bremen, Germany, and the Universidade 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 no. 03F0253A, Mangrove Dynamics and Management—MADAM), and the Conselho Nacional de Pesquisa e Tecnologia (CNPq). We thank 3 anonymous reviewers for their helpful comments.

LITERATURE CITED

- Allen D, Haertel-Borer S, Milan B, Bushek D, Dame R (2007) Geomorphological determinants of nekton use of intertidal salt marsh creeks. *Mar Ecol Prog Ser* 329:57–71
- Allen D, Luthy S, Garwood J, Young R, Dame R (2013) Nutrient subsidies from nekton in salt marsh intertidal creeks. *Limnol Oceanogr* 58:1048–1060
- Ansell A, Gibson R (1990) Patterns of feeding and movement of juvenile flatfishes on an open sandy beach. In: Barnes M, Gibson R (eds) *Trophic relationships in the marine environment*. Aberdeen University Press, Aberdeen, p 191–207
- Brenner M, Krumme U (2007) Tidal migration and patterns in feeding of the four-eyed fish *Anableps anableps* L. in a north Brazilian mangrove. *J Fish Biol* 70:406–427
- Bretsch K, Allen D (2006a) Tidal migrations of nekton in salt marsh intertidal creeks. *Estuar Coasts* 29:474–486
- Bretsch K, Allen DM (2006b) Effects of biotic factors on depth selection by salt marsh nekton. *J Exp Mar Biol Ecol* 334:130–138
- Castellanos-Galindo G, Krumme U (2013) Tidal, diel and seasonal effects on intertidal mangrove fish in a high-rainfall area of the Tropical Eastern Pacific. *Mar Ecol Prog Ser* 494:249–265
- Castellanos-Galindo G, Krumme U, Willis T (2010) Tidal influences on fish distributions on tropical eastern Pacific rocky shores (Colombia). *Mar Ecol Prog Ser* 416:241–254
- Cattrijsse A, Makwaia E, Dankwa H, Hamerlynck O, Hemminga M (1994) Nekton communities of an intertidal creek of a European estuarine brackish marsh. *Mar Ecol Prog Ser* 109:195–208
- Cervigón F, Cipriani R, Fischer W, Garibaldi L and others (1993) FAO species identification sheets for fishery purposes: field guide to the commercial marine and brackish-water resources of the northern coast of South America. FAO, Rome
- Cohen M, Lara R, Szlafsztein C, Dittmar T (2000) Digital elevation model as a GIS tool for the analysis of mangrove coasts, Amazon Region, Brazil. *J Environ Creation* 1: 31–41
- Cohen M, Lara R, Szlafsztein C, Dittmar T, Firme T (2004) Mangrove inundation and nutrient dynamics from a GIS perspective. *Wetlands Ecol Manage* 12:81–86
- Dingle H (1996) *Migration: the biology of life on the move*. Oxford University Press, New York, NY
- Ellis W, Bell S (2008) Tidal influence on a fringing mangrove intertidal fish community as observed by *in situ* video recording: implications for studies of tidally migrating nekton. *Mar Ecol Prog Ser* 370:207–219
- Frias-Torres S, Luo J (2009) Using dual-frequency sonar to detect juvenile goliath grouper *Epinephelus itajara* in mangrove habitat. *Endang Species Res* 7:237–242
- Giarrizzo T, Krumme U, Wosniok W (2010) Size-structured migration and feeding patterns in the banded puffer fish *Colomesus psittacus* (Tetraodontidae) from north Brazilian mangrove creeks. *Mar Ecol Prog Ser* 419:157–170
- Giarrizzo T, Schwamborn R, Saint-Paul U (2011) Utilization of carbon sources in a northern Brazilian mangrove ecosystem. *Estuar Coast Shelf Sci* 95:447–457
- Gibson RN (1973) The intertidal movements and distribution of young fish on a sandy beach with special reference to the plaice (*Pleuronectes platessa* L.). *J Exp Mar Biol Ecol* 12:79–102
- Gibson RN (1980) A quantitative description of the behaviour of wild juvenile plaice (*Pleuronectes platessa* L.). *Anim Behav* 28:1202–1216
- Gibson RN, Pihl L, Burrows MT, Modin J, Wennhage H, Nickell LA (1998) Diel movements of juvenile plaice *Pleuronectes platessa* in relation to predators, competitors, food availability and abiotic factors on a microtidal nursery ground. *Mar Ecol Prog Ser* 165:145–159
- Guest M, Connolly R (2004) Fine-scale movement and assimilation of carbon in saltmarsh and mangrove habitat by resident animals. *Aquat Ecol* 38:599–609
- Hampel H, Cattrijsse A (2004) Temporal variation in feeding rhythms in a tidal marsh population of the common goby *Pomatoschistus microps* (Kroyer, 1838). *Aquat Sci* 66: 315–326

- Hindell J, Jenkins G (2005) Assessing patterns of fish zonation in temperate mangroves, with emphasis on evaluating sampling artefacts. *Mar Ecol Prog Ser* 290:193–205
- Kimball M, Able K (2007a) Tidal utilization of nekton in Delaware Bay restored and reference intertidal salt marsh creeks. *Estuar Coasts* 30:1075–1087
- Kimball M, Able K (2007b) Nekton utilization of intertidal salt marsh creeks: tidal influences in natural *Spartina*, invasive *Phragmites*, and marshes treated for *Phragmites* removal. *J Exp Mar Biol Ecol* 346:87–101
- Kimball M, Able K (2012) Tidal migrations of intertidal salt marsh creek nekton examined with underwater video. *Northeast Nat* 19:475–486
- Kneib R (1991) Flume weir for quantitative collection of nekton from vegetated intertidal habitats. *Mar Ecol Prog Ser* 75:29–38
- Kneib R (1997) The role of tidal marshes in the ecology of estuarine nekton. *Oceanogr Mar Biol Annu Rev* 35:163–220
- Kneib RT (2000) Salt marsh ecoscapes and production transfers by estuarine nekton in the Southeastern United States. In: Weinstein M, Kreeger D (eds) Concepts and controversies in tidal marsh ecology. Springer, Dordrecht, p 267–291
- Kneib RT (2009) Genotypic variation does not explain differences in growth of mummichogs *Fundulus heteroclitus* from simple and complex tidal marsh landscapes. *Mar Ecol Prog Ser* 386:207–219
- Kneib RT, Wagner S (1994) Nekton use of vegetated marsh habitats at different stages of tidal inundation. *Mar Ecol Prog Ser* 106:227–238
- Koch V, Wolff M (2002) Energy budget and ecological role of mangrove epibenthos in the Caeté estuary, North Brazil. *Mar Ecol Prog Ser* 228:119–130
- Kon K, Kurokura H, Tongnunui P (2011) Influence of a microhabitat on the structuring of the benthic macrofaunal community in a mangrove forest. *Hydrobiologia* 671:205–216
- Krumme U (2009) Diel and tidal movements by fish and decapods linking tropical coastal ecosystems. In: Nagelkerken I (ed) Ecological connectivity among tropical coastal ecosystems. Springer, Dordrecht, p 271–324
- Krumme U, Saint-Paul U (2003) Observations of fish migration in a macrotidal mangrove channel in Northern Brazil using a 200-kHz split-beam sonar. *Aquat Living Resour* 16:175–184
- Krumme U, Keuthen H, Saint-Paul U, Villwock W (2007) Contribution to the feeding ecology of the banded puffer fish *Colomesus psittacus* (Tetraodontidae) in north Brazilian mangrove creeks. *Braz J Biol* 67:383–392
- Lee SY (1999) Tropical mangrove ecology: physical and biotic factors influencing ecosystem structure and function. *Austral Ecol* 24:355–366
- McGrath P, Herbert A (2009) Site fidelity, home range, and tidal movements of white perch during the summer in two small tributaries of the York River, Virginia. *Trans Am Fish Soc* 138:966–974
- Meager JJ, Vance DJ, Williamson I, Loneragan NR (2003) Microhabitat distribution of juvenile *Penaeus merguensis* de Man and other epibenthic crustaceans within a mangrove forest in subtropical Australia. *J Exp Mar Biol Ecol* 294:127–144
- Nascimento W Jr, Souza-Filho P, Proisy C, Lucas R, Rosenqvist A (2013) Mapping changes in the largest continuous Amazonian mangrove belt using object-based classification of multisensor satellite imagery. *Estuar Coast Shelf Sci* 117:83–93
- Oliveira V, Fontoura N, Montag L (2011) Reproductive characteristics and the weight-length relationship in *Anableps anableps* (Linnaeus, 1758) (Cyprinodontiformes: Anablepidae) from the Amazon. *Neotrop Ichthyol* 9:757–766
- Raffaelli D, Richner H, Summers R, Northcott S (1990) Tidal migrations in the flounder (*Platichthys flesus*). *Mar Behav Physiol* 16:249–260
- Rangeley R, Kramer D (1995) Tidal effects on habitat selection and aggregation by juvenile pollock *Pollachius virens* in the rocky intertidal zone. *Mar Ecol Prog Ser* 126:19–29
- Rönnbäck P, Troell M, Kautsky N, Primavera J (1999) Distribution pattern of shrimps and fish among *Avicennia* and *Rhizophora* microhabitats in the Pagbilao mangroves, Philippines. *Estuar Coast Shelf Sci* 48:223–234
- Rönnbäck P, Macia A, Almqvist G, Schultz L, Troell M (2002) Do penaeid shrimps have a preference for mangrove habitats? Distribution pattern analysis on Inhaca Island, Mozambique. *Estuar Coast Shelf Sci* 55:427–436
- Rozas L (1992) Bottomless lift net for quantitatively sampling nekton on intertidal marshes. *Mar Ecol Prog Ser* 89:287–292
- Sheaves M (2005) Nature and consequences of biological connectivity in mangrove systems. *Mar Ecol Prog Ser* 302:293–305
- Stevens P, Montague C, Sulak K (2006) Fate of fish production in a seasonally flooded saltmarsh. *Mar Ecol Prog Ser* 327:267–277
- Teo SLH, Able KW (2003) Habitat use and movement of the mummichog (*Fundulus heteroclitus*) in a restored salt marsh. *Estuaries* 26:720–730
- Tyler A (1971) Surges of winter flounder, *Pseudopleuronectes americanus*, into the intertidal zone. *J Fish Res Board Can* 28:1727–1732
- Vance DJ, Haywood MDE, Heales DS, Kenyon RA, Loneragan NR, Pendrey RC (1996) How far do prawns and fish move into mangroves? Distribution of juvenile banana prawns *Penaeus merguensis* and fish in a tropical mangrove forest in northern Australia. *Mar Ecol Prog Ser* 131:115–124
- Vance DJ, Haywood MDE, Heales DS, Kenyon RA, Loneragan NR, Pendrey RC (2002) Distribution of juvenile penaeid prawns in mangrove forests in a tropical Australian estuary, with particular reference to *Penaeus merguensis*. *Mar Ecol Prog Ser* 228:165–177
- Webb SR, Kneib RT (2002) Abundance and distribution of juvenile white shrimp *Litopenaeus setiferus* within a tidal marsh landscape. *Mar Ecol Prog Ser* 232:213–223
- Weinstein M, Litvin S (2000) The role of tidal salt marsh as an energy source for marine transient and resident finfishes: a stable isotope approach. *Trans Am Fish Soc* 129:797–810
- Wothke A, Greven H (1998) Freilandbeobachtungen an Vieraugenfischen, *Anableps anableps* (Anablepidae, Cyprinodontiformes), aus Trinidad. *Z Fischkd* 5:59–75
- Zahl PA, McLaughlin JJA, Gomprecht RJ (1977) Visual versatility and feeding of the four-eyed fishes, *Anableps*. *Copeia* 1977:791–793