

**FEEDING ECOLOGY OF *ANABLEPS ANABLEPS* (ACTINOPTERYGII:
CYPRINODONTIFORMES: ANABLEPIDAE)
OFF THE NORTH-EASTERN COAST OF BRAZIL**

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Background. Diets, feeding ecology, and feeding strategies of several mangrove fish species have not been studied off the coast of Maranhão, which is exposed to a significant tidal regime. This includes also the largescale four-eyed fish, *Anableps anableps* (Linnaeus, 1758). The aim of the presently reported study was to characterize diet, feeding strategies and seasonal patterns of the diet of *A. anableps*.

Materials and methods. The sampling was carried out in São Marcos Bay between May 2007 and April 2008 using block nets. The stomach fullness index was used for stomach content analysis. Dietary items were identified and parameters such as the prey-specific abundance and the frequency of occurrence were calculated. The feeding strategy was analysed with the aid of the Costello diagram. Seasonal patterns in the feeding behaviour and similarity in diet composition were also analysed.

Results. Diet composition did not differ between seasons but stomach fullness was greater in wet season months. The diet of *A. anableps* consisted of a mixture of epiphytic microalgae and macroalgae, insects, crustaceans, molluscs, fishes, and digested material such as mud and detritus. Insects represented the greatest richness among the food items. The Costello diagram revealed that *A. anableps* had a generalist feeding strategy, with a dominance of macroalgae, insect, and fishes. A broad niche was also found, as indicated by a strong association with interphenotypical components.

Conclusion. This study presents data that confirm the forage characteristic of *A. anableps* and the influence of seasonality on its feeding behavior, in which the species takes advantage of the greater availability of food due to runoff and the larger flooded area, during the wet season. Further studies should be carried out to determine the energy needs of this species in satisfying its reproductive demands as well as the abundance of food resources in the surrounding environment and the confirmation of the generalist feeding strategy.

Keywords: diet, four-eyed fish, largescale four-eyed fish, *Anableps anableps*, mangrove creek, Gulf of Maranhão

INTRODUCTION

The geographic distribution of fishes of the family Anablepidae in the Atlantic Ocean is restricted to an area from the Gulf of Paria in Venezuela to the Parnaíba River delta in north-eastern Brazil, where these species

commonly occur on mangrove coasts and tidal flats on the north coast of Brazil (Cervigón et al. 1992, Batista and Rêgo 1996). The family Anablepidae is represented in South America by two brackish water species of the same genus: *Anableps anableps* (Linnaeus, 1758) and

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Anableps microlepis Muller et Troschel, 1844. These fishes can swim on the surface and practically keep half of their bodies out of the water, allowing the exploration of shallow environments near the edge of the water (Borwein and Hollenberg 1973, Oliveira et al. 2006, Brenner and Krumme 2007).

The largescale four-eyed fish, *Anableps anableps* (Linnaeus, 1758), is classified as an estuarine resident species and is relatively abundant in estuaries along the coast of the states of Pará and Maranhão (Brazil) (Krumme et al. 2004, Giarrizzo and Krumme 2007, Carvalho Neta and Castro 2008). According to Brenner and Krumme (2007), it has plastic feeding behaviour due to its use of tide dynamics for movement during foraging activities, and its broad feeding spectrum.

Anableps anableps has an important adaptation in its prey-capture behaviour that applies to the feeding in an aquatic environment and then for the terrestrial environment. In the aquatic environment, *A. anableps* approaches the prey and uses a combination of biting and sucking actions to feed. While on land, however, the fish must position the head and jaws directly above the prey (Michel et al. 2015).

The Brazilian states of Maranhão and Pará share the longest contiguous mangrove coast in the world. A number of studies have addressed different aspects of the biology of the largescale four-eyed fish in the northern coastal region of Brazil in the last 20 years, investigating its population dynamics (Ribeiro and Castro 2003), physiology (Oliveira et al. 2006), and reproductive behaviour (Nascimento and Assunção 2008, Oliveira et al. 2011, Cavalcante et al. 2012). An itemized quantitative assessment of its feeding habits in its natural environment, however, has either not been performed (Ribeiro and Castro 2003) or was published a long time ago (Zahl et al. 1977). Brenner and Krumme (2007) studied tidal and diel dynamics in the feeding of *A. anableps* and assessed the feeding strategy of this species in intertidal mangrove creeks in Pará, northern Brazil, based on samples taken during two lunar cycles at the end of the wet season.

Anableps anableps inhabit mangrove environments along the north-eastern coast of South America. The general ecology of this unique fish species, including detailed quantitative assessments of feeding habits in its natural environment, remains largely unknown (Miller 1979, Ribeiro and Castro 2003). However, intertidal prey availability may vary between seasons in response to changes in salinity, and the diet composition may vary between sites (Ley et al. 1994). While the diets of several mangrove fish species from the Pará coasts have been analysed, it is unclear if these results can be

readily extrapolated to the coast of Maranhão, which is exposed to a slightly more significant tidal regime and lower precipitation than the mangroves of Pará. There are therefore gaps in the knowledge regarding the feeding ecology of this species, and little is known about its diet and the strategies employed for the exploration of food sources.

With the hypothesis that the seasonal patterns influence the feeding of *A. anableps*, the aim of the presently reported study was to characterize the diet, feeding strategies and seasonal patterns of the diet of this species.

MATERIALS AND METHODS

The sampling was carried out in the Bahia de São Marcos (São Marcos Bay, approximately 2°16'48"S, 044°03'36"W), which is spatially delimited by the Brazilian mainland to the west, Maranhão Island to the east and the mouth of the Mearim River to the south (Fig. 1). The geographic features of the bay include deep channels, a large number of sandbanks and the outflow of numerous rivers (Anonymous unpublished*, Palma unpublished**). The climate is tropical, hot and humid, and according to Köppen–Geiger Classification this area has a tropical wet and dry climate (Peel et al. 2007). Temperatures in the region range from 22 to 32°C. Annual precipitation is approximately 2300 mm and the relative air humidity ranges from 77% to 100%, thus contributing to a semi-humid tropical climate (Fisch et al. 1998). The region has two distinct seasons, with a wet first semester (January to February) and a dry second semester (July to December). The maximum amplitude of the semi-diurnal large tides is approximately 7.5 m (Souza Filho 2005).

Specimens of *A. anableps* were collected bi-monthly between May 2007 and April 2008, (three collections in each season). Block nets ranging from 45 to 90 m in length with mesh size ranging from 20 to 40 mm between opposing knots were used. This fishing equipment was placed in creeks and sustained by poles driven into the margins of the mangrove, spaced 2 m apart, and placed across the channel to support the net against the current of the outgoing tide. All the samples were taken in the same location, in the daytime at low tide during the first spring tide of the month.

The specimens were stored in ice. Morphometric measurements such as the total length were determined [cm] and the total weight was recorded [g] using stainless steel callipers and a precision analytical scale (0.01 g), respectively.

The stomachs were extracted, weighed, stored in beakers containing a 10% formalin solution for 24 h and then transferred to a 70% ethyl alcohol solution for

* Anonymous 1972. Cartas de corrente de maré – Proximidades da Baía de São Marcos e portos de São Luís e Itaqui. [Tide charts—The proximity of the Bay of São Marcos and the ports of São Luís and Itaqui.] Centro de Hidrografia da Marinha, São Luís, MA, Brazil. [In Portuguese.]

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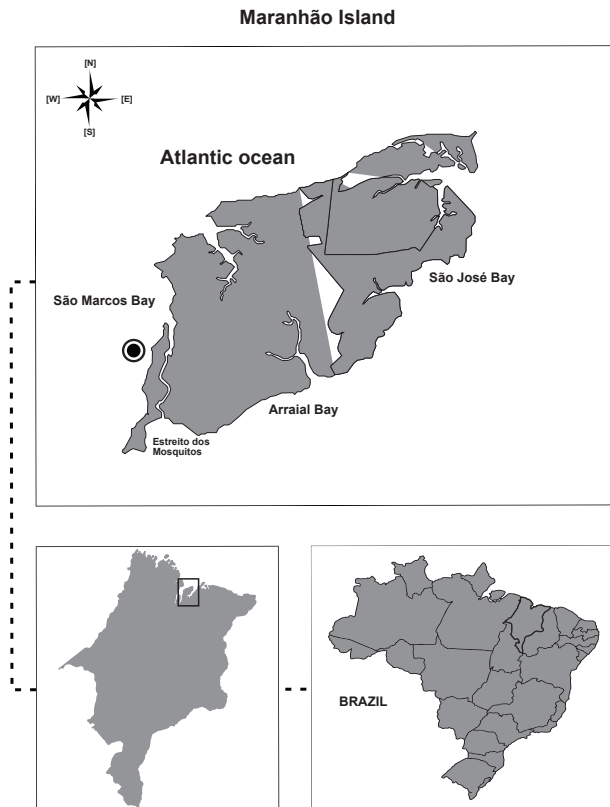


Fig. 1. Map showing the location of the sampling site in São Marcos Bay, Maranhão, Brazil

preservation. The stomach fullness index proposed by Bennemann et al. (2006) was used for stomach content analysis based on the formula

$$GR = (\sum_i \cdot F_A) \cdot F_A^{-1}$$

where i is the degree of attributed repletion; F_A = absolute frequency of individuals with i degree.

The food items were extracted, analysed under a stereomicroscope, and classified based on the degree of digestion, as proposed by Hérran (1988) (digested, semi digested, and undigested). Dietary items were identified to the lowest possible taxonomic level for the acquisition of data on prey-specific abundance (Piorski et al. 2005) and the frequency of occurrence (Yamaguchi et al. 2005).

The feeding strategy of *A. anableps* was analysed with the aid of the Costello diagram modified by Amundsen et al. (1996). In this method, information on the feeding ecology of predators is obtained through a graphic relation between prey-specific abundance ($\%A_i$) and frequency of occurrence ($\%F_i$), calculated using the following formulas:

$$\%A_i = 100S_i \cdot S_i^{-1}$$

$$\%F_i = 100N_i \cdot N^{-1}$$

where S_i is the number of stomachs containing only prey i , S_i is the total number of stomachs in which prey i occurs, N_i is the number of predators with prey i found in stomach, and N is the total number of predators with stomach contents.

For the analysis of seasonal patterns in the feeding behaviour of *A. anableps*, the similarity in diet composition was considered, based on the food items found and the sampling period. A nonparametric graphic representation of multi-dimensional scaling (MDS) (Clarke and Warwick 2001) was constructed after the standardization of the data (frequency of occurrence) and the transformation of the same into square roots to generate a similarity matrix based on Euclidian distances. In the MDS representation, which is a parameter representing the extent to which ordination is related to similarities between samples, stress values < 0.1 correspond to inference within an acceptable margin of safety (Clarke and Warwick 2001).

In order to determine seasonal differences in stomach fullness the Kruskal–Wallis test was utilized after the normality and homogeneity of variances was verified (Zar 1999). All statistical tests used a significance level of 5%.

RESULTS

Degree of fullness. A total of 196 stomachs from *A. anableps* were sampled, of which 105 sampled stomachs were empty. Seasonal variations in the degree of fullness were found. The greatest frequency of completely full stomachs occurred in the wet season months (Kruskal–Wallis, $P < 0.05$). Stomachs that were only 1/4 full were most frequent in June and December 2007 (dry season), whereas half-full stomachs were most frequent in April 2008 (Fig. 2).

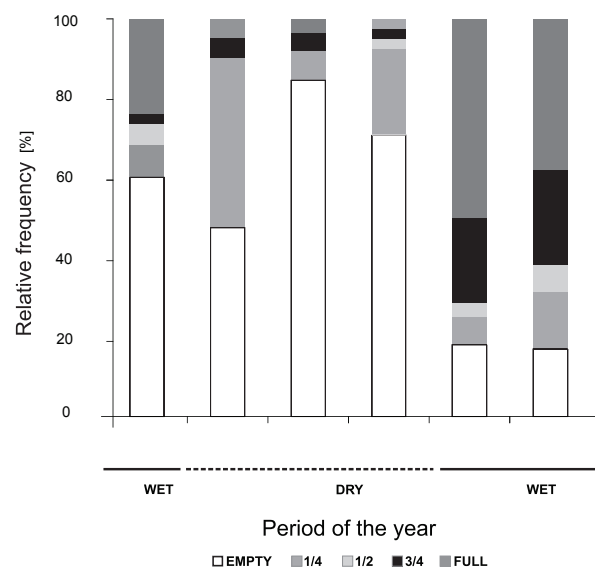


Fig. 2. Stomach repletion index of *Anableps anableps* from São Marcos Bay, Maranhão, Brazil

Food items. The diet of *A. anableps* was composed of six categories: macroalgae, insects, crustaceans, molluscs, fish, and digested matter such as mud and detritus (Table 1). All groups of these items were found in all samples that had stomach content: macroalgae, Insecta, Crustacea, Mollusca, fish and detritus (animals, plants, and inorganic matter). In terms of the relative abundance, detritus was a more numerous item than animals and plants. Insects had the greatest richness among the food items, corresponding to a relative abundance of approximately 17%.

Table 1 DISCUSSION

Specific abundance and frequency indices of food items consumed by *Anableps anableps* from São Marcos Bay, Maranhão, Brazil

Higher taxon/ group	Food item	PI%	FI%
Microalgae		19.90	100.0
Insecta	Coleoptera	5.10	100.0
	Diptera	1.53	50.0
	<i>Drosophila</i> sp.	1.02	33.3
	Homoptera	0.51	16.7
	Hymenoptera	3.57	50.0
	Lepidoptera	2.04	66.7
	Orthoptera	3.57	50.0
Crustacea	Isopoda	1.02	33.3
Mollusca	Gastropoda	2.04	16.7
	<i>Melampus coffeus</i>	1.53	16.7
Actinopterygii		14.29	100.0
Remains	Inorganic mater	12.76	100.0
	Animal detritus	0.51	16.7
	Macroalgae	30.61	100.0

PI% = prey-specific abundance of prey, FO% = relative frequency of prey.

Feeding strategy. The Costello diagram revealed that *A. anableps* had a generalist feeding strategy, with a dominance of macroalgae, insects, and fish. A broad niche was also found, as indicated by a strong association with interphenotypical components (Fig. 3).

Seasonal patterns in diet composition. The MDS ordination formed two groups, differentiated by season. The dry and wet seasons were separated due to the amount of food items ingested, with more food in wet season months and less food during dry season months (Fig. 4).

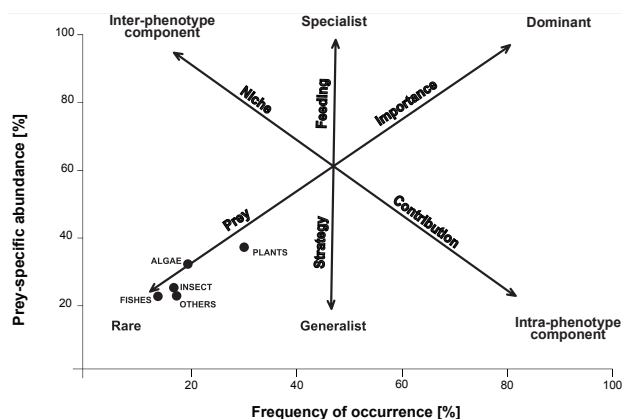


Fig. 3. Diagram of Costello showing the graphical relation between the frequency of occurrence and the prey-specific abundance in the diet of *Anableps anableps* from São Marcos Bay, Maranhão, Brazil

Macroalgae, insects, and fishes (Teleostei) occurred more frequently among the food items of the diet of *A. anableps* from the Bahia de São Marcos (São Marcos Bay), in the state of Maranhão, Brazil. Previous studies have already shown the feeding plasticity of this species and cited other food items not found in the presently reported investigation (Zahl et al. 1977, Brenner and Krumme 2007, Michel et al. 2015), indicating the omnivorous habits of *A. anableps*. An amount of detritus and inorganic matter from the sandy and/or muddy bottom was found in the stomachs of the largescale four-eyed fish, which was likely ingested during foraging activities targeting the benthic organisms associated with non-consolidated bottoms, such as Isopoda and Mollusca. This feeding behaviour was also observed in the diet of *A. anableps* caught in Caeté Bay, Pará, Brazil, although it was of minor importance in such diet (Brenner and Krumme 2007). According to Greven et al. (2002) the mouth of this species is terminal and orientated slightly downwards, and it is assumed that *A. anableps* ingest food from the bottom in shallow water. Gee (1989), Wakabara et al. (1993), and Flynn (1998) stated that the presence of sediment in stomachs may be a strong indication of trophic enrichment in aquatic environments, due to the high density of epifaunal and infaunal benthic organisms.

Mangroves represent an ecosystem with highly complex trophic dynamics, due to the wide range of food items available for fish (Ley et al. 1994, Laegdsgaard and Johnson 2001). Indeed, most Neotropical fishes have insectivorous/omnivorous feeding habits, which is reflected in their feeding plasticity when there is a need to replace one food item with another (Knöppel 1970, Ferreira 1993, Nieder 2001, Lowe-McConnell unpublished*).

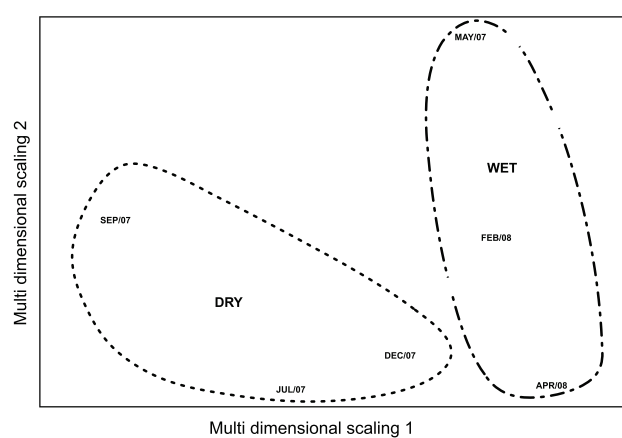


Fig. 4. Graphical representation of the MDS of the similarity of the food composition of *Anableps anableps* captured in the São Marcos Bay, Maranhão, Brazil, in the wet and dry seasons

* Lowe-Mc Connell R.H. 1999. Estudos ecológicos de comunidades de peixes tropicais. [Ecological studies of communities of tropical fishes.] Editora da Universidade de São Paulo, São Paulo. [In Portuguese.]

The feeding strategy employed by *A. anableps* is diversified, which classifies this species as a generalist, as it combines a unique ability to see both above and below the water surface, so simultaneously searching for benthic, nektonic, and planktonic organisms in inundated mangroves during high tide (Zahl et al. 1977), with movement in search of food sources of an autochthonous and allochthonous origin (Brenner and Krumme 2007). According to Brenner and Krumme (2007), this species offers an interesting plant–animal interaction by removing epiphyte coverage from the aboveground mangrove root system, thus fulfilling a mutually beneficial cleaning function. At flood tide, *A. anableps* generally enters mangroves through tidal channels to feed on macroalgae that make up the “Bostrychietum” at high tide, and gradually returns to the main channel on the outgoing tide (Brenner and Krumme 2007), concentrating near the swash zone at low tide (Brenner and Krumme 2007, Nunes JLS pers. obs.). According to Ferry-Graham et al. (2008), *A. anableps* is part of a group of cyprinodontiform fishes known for being ‘picky’ eaters allowing them to select prey items from non-nutritive items.

This species is also known to move and feed in the water column and to jump and feed on mudbanks (Zahl et al. 1977, Brenner and Krumme 2007, Michel et al. 2015). However, according to Michel et al. (2015) individuals of *A. anableps* lack an axial or pectoral mechanism to reorient the mouth ventrally, toward terrestrial prey.

The presence of airborne insects in this study as a food component of *A. anableps* was also reported in a study by Brenner and Krumme (2007), which related the elongated body to acceleration during jumping that probably helps when attacking above-water prey items such as Insecta. This group can also represent an abundant and nutrient-rich food resource for many mangrove fishes (Ley et al. 1994, Krumme et al. 2004). The adaptations of feeding apparatus follow the evolutionary changes in the jaw mechanics allowed more-derived cyprinodontiform fishes the ability to select individual prey items from the water column or substrate, in effect, a picking-based prey-capture mechanism (Ferry-Graham et al. 2008, Hernandez et al. 2009). In *A. anableps*, this feeding mechanism has been extended to allow more protrusion and rotation of the upper jaws (Michel et al. 2015).

The presence of insects in the wet season demonstrates how population dynamics influence the availability of a food source. This also illustrates the opportunistic capacity of the largescale foureyed fish when feeding on an abundant item. Furthermore, environmental changes can force species to temporarily switch to other food items due to the scarcity of a preferred resource (Chaves and Vendel 2008).

A similar situation of opportunism has been documented for coastal species off the state of Maranhão, such as *Genyatremus luteus* (Bloch, 1790), which takes advantage of the high density of the mollusc *Mytella charruana* to feed almost exclusively on this item (Almeida et al. 2005). In contrast, fish with a diet characterized by a limited variety of food items can suffer due to the negative effects of intra- and inter-species competition (Lucena et al. 2000).

The seasonality in the degree of repletion was defined by the greater frequency of full stomachs in the rainy season and empty stomachs in the dry season. This pattern can be in agreement with data from every study on the biology and reproductive ecology of the largescale foureyed fish in Brazil, associating the accumulation of food items in the wet season to the energy demands stemming from the clearer reproductive investment in this season (Ribeiro and Castro 2003, Nascimento and Assunção 2008). However, reproductive activities also occur in the dry season (Ribeiro and Castro 2003, Oliveira et al. 2011, Cavalcante et al. 2012), when stomachs are less full. Indeed, copulation can even occur immediately after the female has given birth (Nascimento and Assunção 2008), evidencing continuous reproduction throughout the year.

On the other hand, the large proportion of empty stomachs may reflect methodological problems, as the method of capture may have influenced this finding due to the possibility that some individuals regurgitated part or all of their stomach contents prior to becoming entangled in the net (Zavala-Camin 1996). A second possible methodological problem regards the inadequate manner in which the specimens were stored for transport to the laboratory for approximately two hours, as freezing does not neutralize the enzymatic action of the digestion process (Zavala-Camin 1996). According to Brenner and Krumme (2007), the quantity of food consumed by this species was clearly influenced by the tide parameters, time of day, and creek location.

Stomach fullness and digestion stage were strongly influenced by the interaction of the tidal and diel cycle, with the fullest stomachs in spring tide-day and neap tide-day inundations and the poorest foraging conditions during nightly neap tides. The species was omnivorous and displayed a generalized feeding strategy.

CONCLUSIONS AND FUTURE PERSPECTIVES

The feeding ecology of *A. anableps* was largely similar to other sites along the mangrove coast of Pará and Maranhão, regions with high tide variation. In the Maranhão coast, where the seasonality is well defined, with two seasons (dry and wet), the biological characteristics alter during these periods, with greater diversity and availability of food in the wet season. Consequently, the species under study takes advantage of this condition, with greater fullness of the stomachs. This was likely due to greater overall intertidal habitat accessibility in the wet season when the levels of intertidal inundation were higher. Increased runoff from rivers during the wet season increases water levels within the estuaries by several decimetres.

It is important to consider the trophic plasticity of this species, which emphasizes the importance of mangroves in the provision of food sources, including vegetal detritus. Further studies should be carried out to determine the energy needs of this species in satisfying its reproductive demands as well as the abundance of food resources in the surrounding environment and the confirmation of the generalist feeding strategy.

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