

Feeding ecology of immature *Lithodoras dorsalis* (Valenciennes, 1840) (Siluriformes: Doradidae) in a tidal environment, estuary of the rio Amazonas

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Studies of feeding ecology are important for the evaluation of interactive processes in fish communities. This study evaluated the feeding ecology of *Lithodoras dorsalis* (Doradidae) from streams within the Amazon estuary delta (Brazil), a macro-tidal area, on different pluviometric periods. A total of 371 young specimens was collected during 12 months of sampling (July 2010 to June 2011). The species diet was composed of 28 food items analyzed by Repletion Index, Alimentary Index and Niche Breadth. Young *L. dorsalis* was classified as herbivore with a frugivory tendency due to the high importance of fruit and seeds in its diet. Food intake varied among sampled months, with the lowest intake being recorded during the rainy-dry season transition period, and the highest at the beginning of the dry season. The importance of food items and the composition of the diet were different throughout the year, probably due to the daily tides that allow fish to access new environments and the pluviometric periods. These results provide important data on the feeding ecology of Amazonian doradids. The study also emphasized the importance of allochthonous resources, derived from the riparian forest, which reinforces the importance of this habitat for the conservation of Neotropical freshwater fishes.

O estudo da ecologia alimentar de peixes é uma abordagem consistente na avaliação dos processos interativos dentro das comunidades. Dessa forma, este trabalho teve como objetivo investigar a ecologia alimentar do bacu-pedra *Lithodoras dorsalis* em furos próximos no delta do estuário Amazônico (Brasil), uma área sobre influência de macro-marés, em diferentes períodos pluviométricos. Durante 12 meses de coletas (julho de 2010 a junho de 2011), foram coligidos 371 espécimes jovens, sendo que a dieta da espécie foi composta por 28 itens alimentares analisados pelos seguintes índices: Índice de Repleção Estomacal, Índice de Importância Alimentar e Amplitude de Nicho. *Lithodoras dorsalis* quando jovem foi classificada como herbívora com tendência à frugivoria, devido aos altos valores de importância de frutos e sementes em sua dieta. A intensidade de obtenção de alimento por *L. dorsalis* diferiu entre os meses de coleta, onde o final do período de transição chuva-estiagem e o início da estiagem foram os períodos de menor e maior atividade alimentar, respectivamente. Também houve diferença na importância alimentar dos itens entre os períodos pluviométricos. Estes resultados fornecem informações importantes sobre a ecologia alimentar de doradídeos na Amazônia. Além disso, percebeu-se o alto consumo de material alóctone pelo bacu-pedra, sendo estes itens alimentares provenientes da floresta ripária, o que reforça a importância deste ambiente para a conservação da ictiofauna neotropical.

Keywords: Diet, Doradidae, Feeding Index, Rock-bacu, Thorny catfish.

Introduction

Studies of feeding ecology are of fundamental importance for the understanding of interactive processes in fish communities (Winemiller, 1989; Hahn *et al.*, 1997; Abelha *et al.*, 2001), including those involving habitat features. In the Neotropics, aquatic environments provide fishes with an ample variety of food items, ranging from invertebrates to fruit and fishes (Goulding, 1980; Lowe-McConnell, 1999). However, the abundance

of these resources may vary considerably over the course of the year, reflecting seasonal fluctuations in rainfall levels or hydrological parameters (Junk, 1980). This limits the degree of ecological specialization of most fish species for a single type of food item. Given this, most Neotropical fish species are dietary generalists or opportunists (Lowe-McConnell, 1999), and present considerable versatility in response to fluctuations in food availability (Abelha *et al.*, 2001; Correa & Winemiller, 2014).

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The vegetation along the stream and rivers provide food and habitat for fish during the flooding period. The flooding may occur irregularly or seasonally by the intense rainfall or daily by the tide (Junk, 1980; Barthem & Schwassmann, 1994; Claro-Jr. *et al.*, 2004; Junk *et al.*, 2012). The rainy period influences also the phenology of growth and reproduction of plants, which may produce fruits in wet or dry season. Fruit and seeds may provide fishes with a valuable source of energy to overcome periods of reduced resource availability and specially to produce their lipid-rich eggs (Goulding, 1980). Fishes may change their diet in response to fluctuations in the abundance of specific resources between climatic seasons (Abelha *et al.*, 2001; Novakowski *et al.*, 2008). Species adapted to frugivory, for example, may be forced to shift the diet and consume leaves, flowers or other plants parts during certain periods, depending on plant phenology patterns and the characteristics of the fish species, such as its energetic demands and body size, among others (Chick *et al.*, 2003; Anderson *et al.*, 2011; Horn *et al.*, 2011). Species such as açai berry (*Euterpe oleracea* Mart.), aninga (*Montrichardia linifera* (Arruda) Schott) and buriti (*Mauritia flexuosa* L.) are abundant on the tidal floodplain of the rio Amazonas mouth. They play a prominent role in the feeding ecology of frugivorous fishes due primarily to the fact that they have asynchronous fruiting periods, and thus provide resources throughout most of the year (Maia & Chalco, 2002; Guimarães *et al.*, 2004; Leão & Carvalho, 2005).

The rock-bacu or bacu-pedra *Lithodoras dorsalis* (Valenciennes, 1840) is one of the largest thorny catfish (Siluriformes, Doradidae), reaching at least 90 cm fork length and 12 kg in weight (Goulding, 1980). The species occurs in northern South America in the Amazon estuary and neighboring coastal areas of French Guiana (Sabaj & Ferraris-Jr., 2003) and it is exploited by the commercial and local fisheries in the Amazon mouth. *Lithodoras dorsalis* eats fruits and seeds and plays a role in the seed dispersal processes (Goulding, 1980; Souza-Stevaux *et al.*, 1994; Waldhoff *et al.*, 1996; Pilati *et al.*, 1999; Maia & Chalco, 2002). This species was classified as omnivorous by Santos *et al.* (2004) and herbivorous by Santos *et al.* (2006), and consumes molluscs, aquatic insect larvae, fruits and seeds (Ringuelet *et al.*, 1967; Santos *et al.*, 2004, 2006).

The goal of this study was to investigate the diet shift throughout the year and the relative importance of food types in the diet of young *Lithodoras dorsalis* in the rio Amazonas estuary, an environment with daily tidal influence and marked pluviometric periods. The species foraging activity was expected to be higher during the rainy period due to the increase in habitats availability because of the greater range of variation in the river levels. This allows the fish to access new environments and resources daily, which does not occur in the dry season.

Material and Methods

Study Area. Data were collected in the municipality of Abaetetuba, in the confluence of the rio Tocantins and rio Pará, in Pará State, Brazil. Rio Pará receives part of the rio Amazonas discharge, which contributes with suspended solids and high turbidity, changes in water level and current direction are directly related to the tidal effect (Sioli, 1984; Barthem & Schwassmann, 1994). The average daily tidal range at Abaetetuba is less than 3 m, but during the equinoxial spring tides and the full or new phases of the moon the tide amplitude reaches 4.0 m (Hida *et al.*, 1999). The limnological characteristics of the water change with the variation of the rio Tocantins discharge. The water is rather transparent during the high discharge period of the rio Tocantins and become turbid in the low discharge period, due to the influence of rio Amazonas waters (Sioli, 1984; Barthem & Schwassmann, 1994).

The vegetation is defined as tidal floodplain vegetation with ombrophilous, broadleaved species, merged with palm trees like buriti tree (*M. flexuosa*) and açai berry tree (*E. oleracea*), the latter being a species of great economic importance for local populations (Machado, 2008). The fruiting period of *E. oleracea* is from July to November (Guimarães *et al.*, 2004), while *M. flexuosa* fruits from March to August (Sampaio & Carrazza, 2012).

The local climate can be classified as Af following the Köppen-Geiger classification, corresponding to the typical conditions of tropical rainforest ecosystems (Peel *et al.*, 2007). Annual precipitation is approximately 2000 mm (Machado, 2008). The rainy season lasts from February to April, rain-drought from May to July, the dry season from August to November and drought-rain from December to January. These periods will be analyzed and related to the feeding of *L. dorsalis*. Mean temperature is 27°C, ranging from 20°C to 35°C over the year. Relative humidity is high, around 85%, varying normally between 81% and 90% (Machado, 2008).

Sampling. *Lithodoras dorsalis* specimens were collected monthly over a year, between July 2010 and June 2011. Specimens were collected in the streams of Sirituba Island in Abaetetuba, Pará, Brazil (01°41'13.6"S 48°52' 48.8"W; Figure 1).

Weir fishing nets of approximately 10 m in length, 3 m in height (30 m² of area), with a between-knots mesh size of 3-6 cm, were used to capture specimens. These nets were set in the stream mouth at dusk (between 17:00 h and 19:00 h), depending on the tide, and removed at dawn (05:00-07:00 h). This period of the day was adopted to ensure the capture of individuals moving from the smaller rivers to the main channel during the low tide. Specimens were removed each two hours from the area using seine nets (5 m x 1 m), and hand- or dip-nets.

The specimens captured were analysed in laboratory conditions in the Federal Institute of Pará (Instituto Federal

do Pará - IFPA), where they were weighed (total weight in grams - W_{total}) and measured from the anterior extremity to the end of the spine (standard length in centimeters - L_{std}). A ventral-longitudinal incision was then made from the urogenital opening to the head for the removal of the stomach, which was weighed (grams) and emptied for the collection of its contents. The contents were weighed separately (grams) and then sorted in a Petri dish. Each distinct food item was identified using a stereomicroscope

(40 x), and weighed separately. The gonads of each specimen were also removed for the definition of maturation phases.

Following evisceration, the specimens were fixed in 10% formaldehyde, conserved in 70% alcohol, and then incorporated into the ichthyological collection of Museu Paraense Emílio Goeldi (MCT/MPEG), under the following catalog numbers: MPEG19134; MPEG19202; MPEG19203; MPEG19610; MPEG19611; MPEG21668-MPEG21681.

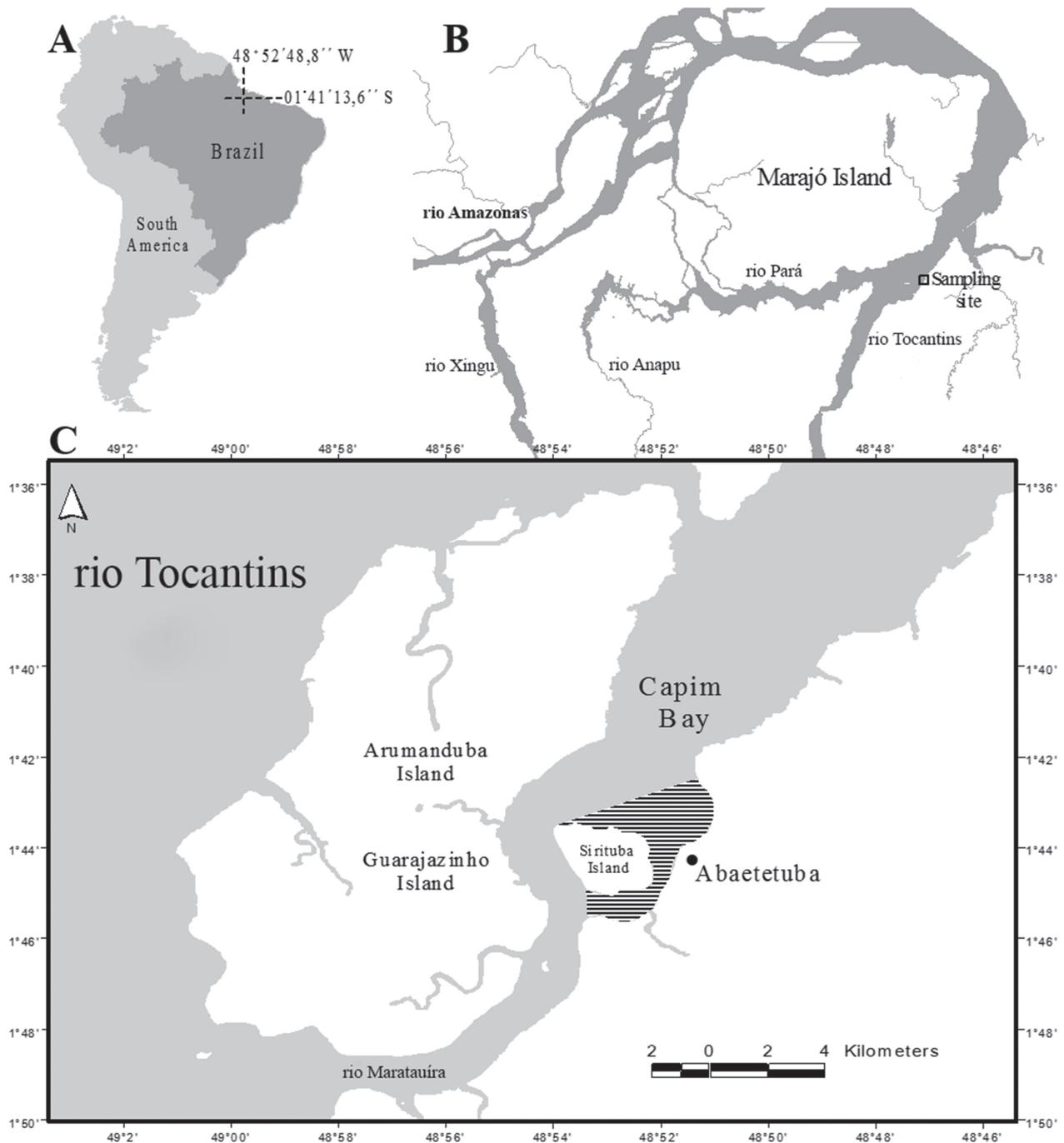


Fig. 1. Location of study area near the mouth of the rio Amazonas in Brazil. A, Location of Brazil on South America; B, rio Amazonas mouth with the sampling site; C, Study area (specimens were collected within the shaded area).

Data analysis. The *Lithodoras dorsalis* diet composition was inferred by analyzing stomach contents. Each food item was initially classified as to its origin (allochthonous or autochthonous) and taxonomy. Prey was identified to the lowest possible taxonomic level, depending on the current digestion degree, with the assistance of specialists and appropriate literature (Ruppert *et al.*, 2005; Costa *et al.*, 2006).

The Repletion Index (RI%; Zavala-Camin, 1996) was calculated to verify feeding activity levels. This parameter is obtained by $RI\% = (W_i / W_t) * 100$, where: W_i represents total items weight and W_t total specimen weight. We used a Kruskal-Wallis nonparametric analysis of variance (H), with a 5% significance level, to assess differences in food ingestion rates (RI%) between pluviometric periods.

The relative contribution of different food items to the species' diet was assessed based on the Frequency of Occurrence (FO_i%; Hyslop, 1980), the percentage of stomachs in which each item occurred relative to total number of items, and on the Relative Weight (W%; Hynes, 1950), the weight percentage of each item relative to the weight of all analysed food items (Hyslop, 1980; Zavala-Camin, 1996). FO_i% and W% values were combined to estimate the Alimentary Index (AI_i%, modified from Kawakami & Vazzoler, 1980), which provides a measure of the importance of each food item. This index is calculated as $AI_i\% = (FO_i\% * W\% / \sum FO_i\% * W\%) * 100$, where: AI_i% represents the food item *i* alimentary index, FO_i% the item *i* frequency of occurrence and W% the relative weight of item *i*. Empty stomachs were not considered for this analysis.

To assess the diet shift of *L. dorsalis* among pluviometric periods, the AI_i% values recorded for each item in the different seasons were log (X + 1) transformed. The data were then analyzed using Non-metric Multidimensional Scaling (NMDS) based on the Bray-curtis similarity index of the transformed data (Clarke & Warwick, 2001). AI_i% values were evaluated using an Analysis of Similarity (ANOSIM), with a 5% significance level. A Similarity Percentage Analysis (SIMPER; Clarke & Warwick, 2001) was then performed to identify which items predominated in the different seasons.

Trophic niche breadth was calculated using Levin's standardized index in order to describe changes in the level of dietary specialization relative to pluviometric periods. This index varies from zero, when a species consumes a single type of food category, to one, when it consumes all available foods in equal amounts (Hulbert, 1978). The index is calculated by $Bi = [(\sum_j P_{ij}^2)^{-1}] (n-1)^{-1}$, where: Bi is the standardized trophic niche; P_{ij} is the ratio of the food category *j* on species' *i* diet; and *n*, the total number of food categories. To improve graphic visualization, the trophic niche breadth was calculated using month data, however the pluviometric periods were shown.

Results

During the 12 months of the study period, 371 specimens of sexually immature *Lithodoras dorsalis* were captured. The mean standard length of these specimens was 15.40 cm (SD± 4.87cm) and mean weight was 94±149.45 g. Four of the specimens had empty stomachs, and were not included in the AI_i% analyses. The stomachs sample size per month and season are shown in Table 1.

Table 1. Number of stomachs sampled, per month and pluviometric periods, of *Lithodoras dorsalis* at the rio Amazonas mouth, Brazil, from July 2010 to June 2011.

Month/Period	Number of stomachs sampled
July/10	20
August/10	40
September/10	40
October/10	30
November/10	30
December/10	30
January/11	31
February/11	25
March/11	27
April/11	37
May/11	27
June/11	34
Rain-Drought	81
Dry	140
Drought-Rain	61
Rainy	89
Total	371

Foraging intensity, as measured by the Repletion Index (RI%), varied significantly between seasons ($H_{3,368} = 17.81$; $p < 0.05$). The dry season returned the lowest and the highest value RI% (Median = 7.899; Max. = 23.084 and Min. = 0; Figure 2). Significant differences were also identified in the post-hoc multiple comparisons conducted for the Kruskal-Wallis test (Table 2). In particular, the dry season was significantly different from rain-drought and rainy seasons, showing higher values.

A total of 28 food items were identified (Table 3), of which 16 were allochthonous and 12 autochthonous. In general, açai fruit (*E. oleracea*) was the most important item in *Lithodoras dorsalis* diet (AI_i% = 48.681%), followed by plant fragments (AI_i% = 14.157%) and aninga (*M. linifera*) (AI_i% = 13.179). Per pluviometric periods, *M. linifera* was the main food item consumed in the drought-rain period (AI_i% = 37.677%), *E. oleracea* in dry and drought-rain periods (AI_i% = 79.041 and 44.871, respectively) and plant fragments in the rainy season (AI_i% = 24.715). According to the Alimentary Index (AI_i%), *L. dorsalis* feeds mainly on plant material, in particular fruit and seeds. However, items such as brachyurans, decapods (Paleomonidae), and gastropods were also consumed (see Table 3).

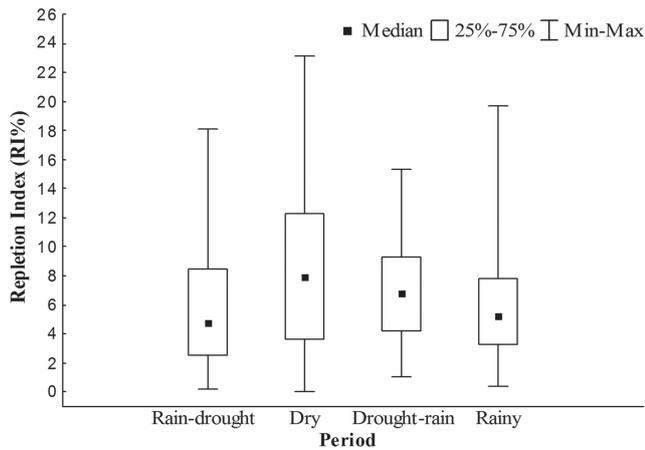


Fig. 2. Box-plot of *Lithodoras dorsalis* Repletion Index (RI%) at the rio Amazonas mouth, Brazil, from July 2010 to June 2011.

Table 2. Probability values for pair-wise comparisons of the Repletion Index (RI%) among pluviometric periods for the rock-bacu *Lithodoras dorsalis*, sampled in the rio Amazonas mouth region, Brazil. (*) Significant values.

	Rain-drought	Dry	Drought-rain	Rainy
Rain-drought				
Dry	0.001*			
Drought-rain	0.195	1.000		
Rainy	1.000	0.010*	0.543	

The NMDS and ANOSIM analyses based on the Alimentary Index (AI_i%) of all items in the diet showed differences in the importance of food items in relation to pluviometric periods (ANOSIM: R = 0.38; p < 0.05) (Figure 3), with clear separation between dry and rainy seasons. The SIMPER analysis revealed that items such as *M. linifera*, *E. oleracea*, *M. flexuosa* and brachyura were responsible for differences among seasons (Table 4).

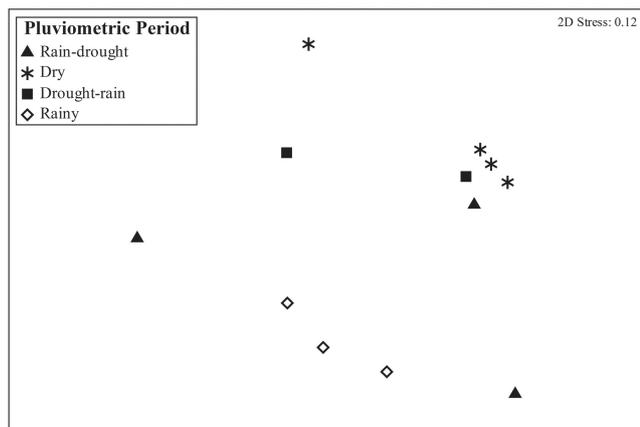


Fig. 3. Non-metric Multidimensional Scaling based on the Alimentary Index (AI_i%) of all food items consumed by the rock-bacu *Lithodoras dorsalis* among pluviometric periods, rio Amazonas mouth region, Brazil.

Table 3. Alimentary Index (AI_i%) per pluviometric period of food resources consumed by the rock-bacu *Lithodoras dorsalis* on the rio Amazonas mouth region, Brazil. (-) Represents the absence of the food item.

Origin	Food Items	Rain-drought	Dry	Drought-rain	Rainy
Allocthonous	Formicidae	0.001	<0.0001	<0.0001	0.001
	Isoptera	0.014	-	-	0.003
	Diptera	-	-	-	0.001
	Diplopoda	0.001	-	<0.0001	<0.0001
	Arthropod Fragment	0.002	<0.0001	0.001	0.011
	<i>Euterpe oleracea</i> Mart.	18.274	79.041	44.871	16.539
	<i>Mauritia flexuosa</i> Mart.	0.846	1.187	11.617	13.029
	<i>Montrichardia linifera</i> (Arruda) Schott	37.677	0.108	0.078	24.391
	Fruit fragments	1.590	1.688	0.712	3.150
	<i>Zea mays</i>	-	<0.0001	-	-
	<i>Anacardium occidentale</i> L.	-	0.001	-	-
	<i>Spondias mombin</i> L.	-	-	0.090	0.019
	<i>Mangifera indica</i> L.	-	-	0.216	-
	Other plant fragments	8.561	9.471	13.744	24.715
	Flowers	0.455	0.107	0.038	0.102
	Leaves	0.026	0.151	-	-
	Autocthonous	<i>Ucarapax</i> and <i>Armases benedict</i>	11.125	3.196	11.125
<i>Macrobrachyum amazonicum</i>		0.127	0.183	0.048	0.133
Gastropoda		0.197	0.001	10.725	0.480
<i>Paxyodon syrmatophorus</i> and <i>Triplodon corrugatus</i>		0.304	0.004	1.273	0.343
Sponges (Demospongiae)		-	-	-	<0.0001
Chironomidae Larvae		<0.0001	<0.0001	-	-
Coleoptera Larvae		-	<0.0001	0.030	0.002
Ciclorapha Larvae		-	<0.0001	-	-
Ephemeroptera Nymph		-	<0.0001	-	-
Oligochaeta		-	<0.0001	-	-
Fish fragments		0.001	0.022	0.001	0.009
Algae		2.174	0.120	0.581	1.131
Digested organic material		12.587	4.660	1.977	1.201
Substrate	6.038	0.001	0.261	2.192	
Minerals	<0.0001	0.059	2.612	1.620	

The trophic niche breadth showed low seasonal variation in resource use by *Lithodoras dorsalis* (Figure 4), since this index ranges from 0 to 1 and the highest value was 0.13 in January. This species has a specialist behavior tendency, with narrow niche breadth, mainly in the beginning of dry season, on 2010, and at the end of the drought-rain transition period, on 2011, due to the high consumption of acai *E. oleracea* (AI_i% = 89.89%) and *M. linifera* (AI_i% = 84.41%), respectively.

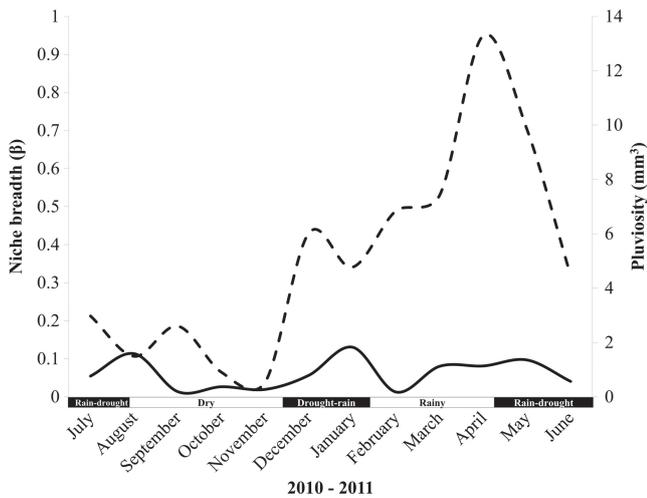


Fig. 4. Trophic niche breadth recorded for *Lithodoras dorsalis* on the rio Amazonas mouth, Pará, Brazil, from July 2010 to June 2011. The solid line represents the niche breadth values and the dashed line indicates mean pluviosity registered for the studied region.

Table 4. Percentage contribution of the main resources consumed by *Lithodoras dorsalis* at Abaetetuba, south of the rio Amazonas estuary (Brazil), during the different pluviometric seasons, based on the results of the SIMPER analysis.

Period	Items	% of Contribution
Rain-drought	<i>Montrichardia linifera</i> (Arruda)	35.1%
	Schott (Aninga)	
	Brachyura	20.6%
	Plant Fragment	20.1%
Dry	<i>Euterpe oleracea</i> Mart. (Açaí Berry)	50.2%
	Plant Fragment	26.3%
	Brachyura	10.2%
Drought-rain	<i>Euterpe oleracea</i> Mart. (Açaí Berry)	27.3%
	<i>Mauritia flexuosa</i> Mart. (Buriti)	23.6%
	Plant Fragment	23.0%
Rainy	<i>Montrichardia linifera</i> (Arruda)	37.6%
	Schott (Aninga)	
	Plant Fragment	28.2%
	<i>Mauritia flexuosa</i> Mart. (Buriti)	21.6%

Discussion

The dominance of young individuals at the rio Amazonas mouth region is because the rock-bacu is a migratory fish with different feeding and reproductive sites. The rio Amazonas mouth is its nursery or growth area, and upstream sections of the rio Amazonas (including tributaries), the reproduction area (Goulding, 1980; Goulding *et al.*, 1996; Barthem *et al.*, 1991). Growth areas, essential for migrating species such as *L. dorsalis*, are sites where young individuals meet food and shelter needs all year long and are able to invest on body growth until

attain sexual maturity, when they migrate to other regions (Goulding, 1980; Barthem *et al.*, 1991). The rio Amazonas mouth has a high food availability, because most plant species fructify on different times, providing fruits and seeds for *L. dorsalis* almost all year long (Guimarães *et al.*, 2004; Leão & Carvalho, 2005; Sampaio & Carrazza, 2012). In addition, because the water variation in the region is determined by the tides, fruits are accessible daily as they fall on the water surface (Barthem & Schwassmann, 1994; Hida *et al.*, 1999).

The high presence of fruits and seeds, like *E. oleracea*, *M. linifera*, *M. flexuosa*, highlights the importance of riparian forests as a substantial food source for Amazonian fishes (Goulding, 1980). Many studies demonstrate the importance of these food items for the ichthyofauna, as a consequence of its high energy level (Hahn *et al.*, 1992; Waldhoff *et al.*, 1996; Winemiller & Jepsen, 1998; Claro-Jr. *et al.*, 2004; Galetti *et al.*, 2008; Pollux, 2011; Correa & Winemiller, 2014). However, the variation in resource availability among pluviometric periods may modify species diet, where most fish species may alter their feeding behaviors according to changes in resource relative abundance (Abelha *et al.*, 2001). The fish fauna of the Amazon basin present a number of specific adaptations to maximize the ingestion of energy according to major seasonal fluctuations in resource availability, for instance the opportunistic feeding behavior (Junk, 1985; Lowe-McConnell, 1999). This pattern was recorded for young *L. dorsalis*, here considered herbivore with a high frugivory tendency. The species fed mainly on fruits and seeds (almost 85% of total AI₁%), according to the phenology of these plants, but also consumed items such as Crustacea and Gastropoda on different times of the year, based on the availability of these invertebrates on the environment. The herbivorous behaviour with high frugivory tendency of adult *L. dorsalis* was also observed by Goulding (1980) in the rio Madeira.

The preference for a given food item due to its availability may be explained by the Optimal Foraging Theory (MacArthur & Pianka, 1966), which predicts that species will choose resources to combine high ease of capture with large amount of energy obtained. Therefore, during the year, species may present a specialist or generalist behaviour in obtaining food resources, depending on availability (Abelha *et al.*, 2001; Wolff *et al.*, 2009; Mazzoni *et al.*, 2010; Masdeu *et al.*, 2011; Correa & Winemiller, 2014). Considering the low taxonomic variety of items ingested, *L. dorsalis* exhibited a behaviour tending to specialist, eating principally fruits and seeds from the riparian forest, varying the species consumed probably according to availability. Furthermore, the presence of sediments in the stomach of *Lithodoras dorsalis* specimens indicates that the species also forages on the bottom, where it obtains the bivalves (mussels and oysters) consumed (Beasley, 2001; Hohn & Costa, 2002). This type of foraging behavior has also been recorded in other doradid species (*e.g.*, Hahn *et al.*, 1997; Lowe-McConnell, 1999). Species of this family

explores all environments searching for food, such as the surface to eat floating fruits, although it is adapted to live in river bottoms.

In view of the discussion above, food availability among pluviometric periods probably influenced *L. dorsalis* feeding intensity (RI%) and its diet composition along the year at the rio Amazonas mouth. The different fructification periods among plant species influence which fruit is consumed during pluviometric periods, changing its foraging behavior (more or less specialist). In addition, the daily variation of water level due to tides is a factor that influences the availability of usable areas by fish populations (Morton *et al.*, 1987; Krumme *et al.*; 2004, Stevens *et al.*, 2010), since the daily flooding of riverbanks allows fishes to reach resources outside the main channel everyday. It does not occur in environments influenced only by seasonal flood pulses; in such areas, fruits are available for fishes only during flooding periods, few months of the year (Goulding, 1980), or in sites where trees are near the river (Anderson *et al.*, 2011; Horn *et al.*, 2011). In conclusion, allochthonous items, especially those of vegetal origin, are important for *Lithodoras dorsalis* as a food source. It highlights the importance of riparian forest conservation at the rio Amazonas mouth, a key source of food resources for Neotropical fishes.

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