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# Feeding ecology of electric eel *Electrophorus varii* (Gymnotiformes: Gymnotidae) in the Curiaú River Basin, Eastern Amazon

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In this study, the composition of the diet and the feeding activity of *Electrophorus varii* were evaluated. The influence of ontogeny and seasonality in these feeding parameters was also examined. Fish were collected in the Curiaú River Basin, Amazon, Brazil, from March 2005 to February 2006, during the rainy (January–June) and dry (July–December) seasons. Diet composition was characterized based on the analysis of stomach contents and feeding dynamics was assessed based on the Stomach Fullness Index (IR) calculated using stomach weight. Stomach content and RI data were grouped into four-cm size classes (40–80, 80–120, 120–160, and 160–200) and two seasonal periods (rainy and dry). The influence of ontogeny and seasonality in the diet was investigated through PERMANOVA, and in the food dynamics through ANOVA. The analysis of stomach contents revealed that fish were the most consumed preys by electric eels, especially Callichthyidae and Cichlidae. Diet composition and RI values of electric eels were not influenced by ontogeny and seasonality. Electric eels are fish predators, regardless of size class and seasonal period.

Keywords: Amapá, Electric fish, Feeding Activity, Floodplain, Piscivory.

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Neste estudo foram avaliadas a composição da dieta e a atividade alimentar de *Electrophorus varii*. A influência da ontogenia e da sazonalidade nestes aspectos da alimentação dos poraquês também foi examinada. Os peixes foram coletados na Bacia do rio Curiaú, Amazônia, Brasil, no período de março de 2005 a fevereiro de 2006, abrangendo os períodos chuvoso (janeiro–junho) e o seco (julho–dezembro). A dieta foi avaliada por meio da análise dos conteúdos estomacais e a dinâmica alimentar por meio do Índice de Repleção Estomacal (RI) baseado nos dados de peso do estômago. Os dados do conteúdo estomacal e do RI foram agrupados em quatro classes de tamanho em cm (40–80, 80–120, 120–160 e 160–200) e dois períodos sazonais (chuvoso e seco). A influência da ontogenia e da sazonalidade na dieta foi investigada por meio da PERMANOVA, e na dinâmica alimentar por meio da ANOVA. A análise do conteúdo estomacal mostrou que os peixes foram as presas mais consumidas pelos poraquês, especialmente Callichthyidae e Cichlidae. A composição da dieta e os valores de RI dos poraquês não foram influenciadas pela ontogenia e pela sazonalidade. Os poraquês são predadores piscívoros, independente da classe de tamanho e do período sazonal.

Palavras-chave: Amapá, Atividade Alimentar, Peixe elétrico, Piscivoria, Planície Inundável

## INTRODUCTION

Fish of the order Gymnotiformes are known for their specialized organs that generate electric discharges for electrolocation and electrocommunication (Moller, 1995). These electric fishes have a geographical distribution confined to freshwater ecosystems in the neotropics, from southern Mexico to northern Argentina (Albert, 2001), inhabiting lakes, wetlands, streams, and rivers (Crampton, 2011). The most notorious Gymnotiformes are electric eels, *Electrophorus* Gill, 1864, because of their strong electric discharges, large size (up to 2.5 meters in total length; Ellis, 1913; Campos-da-Paz, 2003), and air breathing through a modified oral organ (Johansen *et al*., 1968).

Until recently, *Electrophorus* was considered monospecific, with *Electrophorus electricus* (Linnaeus, 1766) as the only valid species (*e.g*., Mago-Leccia, 1994; Ferraris *et al*., 2017), which was refuted by de Santana *et al.* (2019). These authors described two new species: *Electrophorus varii* and *Electrophorus voltai*. *Electrophorus electricus* and *E. varii* generate electric discharges of *ca*. 650 volts, while *E. voltai* can produce discharges of up to 850 volts, making it the strongest bioelectricity generator in the world (de Santana *et al*., 2019). The electric discharges of *Electrophorus* can reach a frequency of up to 500 Hz, and are used in defense against predators and for hunting preys (Bauer, 1979; Catania, 2019). The anatomy and physiology of the electric organs of electric eels are well known (Hunter, 1775; Williamson, 1775; Bauer, 1979; Catania, 2014); however, little information is available on the basic biology of *Electrophorus* species in their natural environment (Sachs, 1881; Ellis, 1913; Assunção, Schwassmann, 1995; Sá-Oliveira, Mendes-Junior, 2012; Mendes-Junior *et al*., 2016).

The information available on the diet of electric eels is speculative, as few stomach contents have been analyzed (Saul, 1975; Soares *et al*., 1986; Planquette *et al*., 1996; Oliveira *et al*., 2019), in addition to a lack of consensus about the feeding habits of *Electrophorus*. Some authors classify *Electrophorus* as specialized fish predators (Bullock *et al*., 1979; Soares *et al*., 1986; Westby, 1988; Mago-Leccia, 1994; Stoddard, 1999; Sá-Oliveira *et al*., 2014; Mendes-Júnior *et al*., 2016), while others have categorized them as generalist carnivores (Ellis, 1913; Sterba, 1959; Saul, 1975; Goulding *et al*., 1988; Planquette *et al*., 1996; Mérona, Rankin-de-Mérona, 2004; Crampton *et al*., 2013; Giora *et al*., 2014; Oliveira *et al*., 2019; Stoddard *et al*., 2019). Nakashima (1941) and Goulding (1980) have also reported the consumption by electric eels of fruits of açaí, *Euterpe oleracea*, a palm tree common in Amazonian floodplains.

Electric eels are important components of the ichthyofauna in Amazonian floodplain systems (Crampton, 1996), where most fishes inhabit the main river channel and feed on a wide variety of preys (Junk *et al*., 1997). During the rainy season, the water level of rivers and their tributaries increases and floods marginal terrestrial habitats, influencing prey availability and quality (Junk *et al*., 1997). Fishes species that inhabit the main river channel and its tributaries migrate to the adjacent floodplains during the rainy season, where they feed and reproduce, with these areas serving as natural nurseries for juveniles of species with general feeding habits (Junk *et al*., 1997; Abelha *et al*., 2001) that then return to the main river channel in the beginning of the dry season. Some fish are trapped in puddles in the floodplain during the dry season, where they usually have carnivorous feeding habits (Junk *et al*., 1997). Individuals of *E. varii* are generally found in residual pools during the dry season that they share with other fish with adaptations to environments with low dissolved oxygen in the water, such as *Hoplosternum littorale* (Hancock, 1828) and *Hoplerythrinus unitaeniatus* (Spix & Agassiz, 1829) (Val *et al*., 1998).

To understand the feeding ecology of fishes species in dynamic ecosystems such as floodplains, it is essential to study parameters other than diet, such as feeding dynamics. Temporal variation in stomach volume can be a useful indicator of patterns and degree of both daily and seasonal fish feeding (Eliassen, Jobling, 1985) and is among the most common methods for estimating prey consumption by fish in the wild (Elliot, Persson, 1978). The analysis of feeding dynamics allows the characterization of the period of feeding activity and the nutritional condition of fish in natural conditions (Barbieri, Barbieri, 1984), as well as the response of fish populations to changes in environmental conditions (Pereira *et al*., 2016). No information is available on the feeding dynamics of *Electrophorus* species in nature, and their period of feeding activity is still unknown.

Fishes diet and feeding activity are influenced by several biotic and abiotic factors, including ontogeny (Griffiths *et al*., 2009; Ferriz, Iwaszkiw, 2014) and changes in hydrometric level (Junk *et al*., 1997). Generally, young fish of predatory species tend to consume a wider variety of prey than adults (Winemiller, 1989; Hahn *et al*., 1997; Novaes *et al*., 2004). These ontogenetic differences in diet are also observed in some species of predatory fishes in floodplains, with small individuals consuming microcrustaceans, medium size fish eating mostly aquatic insects, and larger individuals preying mainly on fish (Winemiller, 1989). Ontogenetic variations in the diet of fry and juveniles of *E. varii* were observed in the floodplain of Ilha do Marajó-PA, Brazil, with 7 cm fish exclusively feeding on conspecific eggs and developing embryos (cannibalism), 8 cm fish consuming mainly of eggs and embryos, with occasional ingestion of crustacean larvae, and 9 cm fish eating mostly crustacean larvae (Assunção, Schwasmann, 1995).

The diet of *E. varii* individuals larger than 9 cm is still unknown.

Some fishes diets and feeding dynamics change seasonally in floodplain ecosystems depending on the availability of food resources, with more autochthonous prey during the dry season and allochthonous ones during the rainy season, with predator fish displaying opportunistic behavior as their main feeding strategy in this type of habitat (Cardoso *et al*., 2019). Therefore, electric eels that inhabit floodplain systems might have higher trophic plasticity, due to greater availability of prey. However, electric eels might also maintain a more specialized feeding habit in floodplains, as electric discharges allow them to hunt more specific preys regardless of the time of year. The present study aims to characterize for the first time the diet of the electric eel *E. varii* in the wild, based on analysis of stomach contents and intestine size, and its feeding dynamics based on stomach weight variation (stomach repletion index – RI), in addition to determining the influence of ontogeny and seasonality in the stomach content and the feeding activities of this species in the Curiaú River basin, Amapá, Brazil.

## MATERIAL AND METHODS

The river-floodplain system of the Curiaú River Environmental Protection Area (Curiaú River EPA) (Fig. 1) is located in the urban expansion area of the Municipality of Macapá, state of Amapá, Brazilian Amazon (Chellappa *et al*., 2005). It covers a small area of 23,000 ha, which contrasts with its high diversity of ecosystems such as savannas, dry-land forests, forests, and floodplains. The Curiaú River and its floodplain form a floodplain-river system, with dry seasons occurring from July to December, and rainy seasons, from January to June (Chellappa *et al*., 2005).

Sampling was carried out mainly in streams, temporary and permanent lakes of the Curiaú River floodplain, which covers most of the Curiaú River EPA. This area has an ichthyofauna dominated by small characids (*Hyphessobrycon* Durbin, 1908 and *Hemigrammus* Gill, 1858; Gama, Halboth, 2003), armored catfishes (*Hoplosternum* Gill, 1858 and *Megalechis* Reis, 1997), and cichlids (*Aequidens* Eigenmann & Bray, 1894 and *Apistogramma* Regan, 1913; Chellappa *et al*., 2005). Temporary lakes of the Curiaú River EPA have several fish with adaptations to low dissolved oxygen concentration, such as aimaras (*Hoplerythrinus* Gill, 1896) and marbled swamp eels (*Synbranchus* Bloch, 1795; Chellappa *et al*., 2005). Electric eels are common in the Curiaú River EPA (Chellappa *et al*., 2005), with *E. voltai* and *E. varii* occurring in the area. The later is the most common electric eel species in the Curiaú River EPA (de Santana *et al*., 2019).

*Electrophorus varii* specimens were sampled every two months, which included the dry (July to December 2005) and the rainy seasons (March 2005 to June 2005 and January and February 2006). Most individuals were collected by active search in the floodplain, using trawl nets, fishing nets, casting nets, and line and hooks at various points distributed in streams, permanent and temporary lakes of the Curiaú River Basin. Groups of gillnets (mesh of 3–10 cm between opposing knots) were set up overnight (12 hours of exposure). The difficulty in locating electric eels in the wild without the use of electric fish detectors, as described by Crampton *et al.* (2007), was offset by the assistance of quilombolas (current inhabitants of rural communities formed by descendants of enslaved Africans), not allowing the pre-establishment of fixed sampling units. Thus,

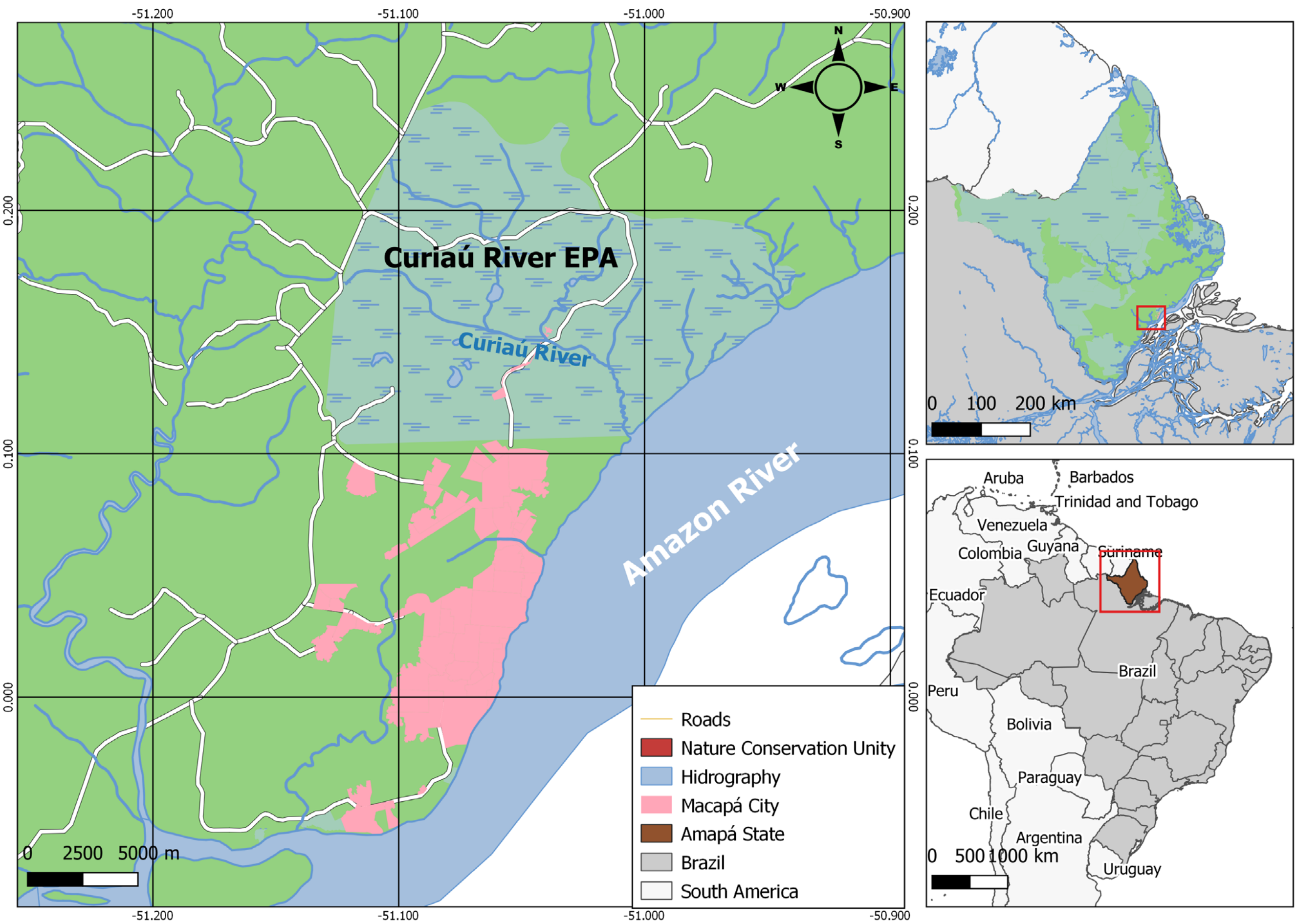


**FIGURE 1** | Study area: Curiaú River Environmental Protection Area in Macapá, Amapá, Brazil.

the entire floodplain with its streams, temporary and permanent lakes was included the study area.

Ninety-five (45–178 cm in length) young (<85 cm, N=20) and adult (>85cm, N=75) electric eels were collected. Of the 95 specimens, 50 were collected in the dry (45–178 cm in length) and 45 in the rainy season (48–163 cm in length). Total weight (Wt) in grams (g) and total length (Lt) in centimeters (cm) were obtained. Fish were dissected, and intestine length (Li) in centimeters (cm) and stomach weight (Ws) in grams (g) were measured. Two intestines were damaged, and their length could not be measured. Voucher specimens were deposited in the biological collection of the Instituto Nacional de Pesquisas da Amazônia (INPA) under numbers INPA 41112 to 41122 and 41124. Stomachs were stored in 10% formalin solution. In order to determine the diet of electric eels, 47 stomachs were dissected with the aid of a stereoscopic microscope. Four were empty and of the 43 stomachs with preys, 15 had damaged identification tags and the information on size and period of collection could not be retrieved. The remaining 28 stomachs belonged to specimens with sizes ranging from 56 to 178 cm in length. Food items were identified at the lowest possible taxonomic level and grouped into the following taxonomic and ecological categories: fish (whole animals in varying degrees of digestion, scales and bones), terrestrial insects (Hymenoptera, Coleoptera and insect remains), aquatic insects (Odonata larvae and Coleoptera), crustaceans (Palaemonidae shrimps and Trichodactylidae crabs), amphibians (frogs), and seeds. Plant remains were not considered as food items as they were probably accidentally ingested while eating other preys and are not commonly observed in stomach contents of other Neotropical electric fishes species (Giora *et al*., 2014).

Food items were analyzed using the occurrence frequency method (Hynes, 1950; Hyslop, 1980; Bowen, 1983) and the Volumetric Analysis Index (Lima-Junior, Goiten, 2001). The importance of each food item was determined by the Alimentary Index (Kawakami, Vazzoler, 1980) as follows: $IAi = (Fi\% \times Vi\%) / (\sum Fi\% \times Vi\%)$, where i = 1,2 , ... n food item, Fi% is the frequency of occurrence of food item i, and Vi% is the volume of food item i.

As a complementary analysis to characterize the diet of electric eels, the Intestinal quotient (IQ), which represents the ratio of intestine length (Li) to total length (Lt), was obtained according to Giora *et al.* (2005) as follows: $IQ = Li / Lt$, where IQ is the intestinal quotient, Li is the intestine length and Lt, total length.

To determine the feeding dynamics of electric eels, the stomach repletion index (RI), calculated as the ratio of stomach weight to total animal weight, was used and estimated according to the formula proposed by Santos (1978) and adapted as in Giora *et al.* (2005): $RI = Ws \times 100 / Wt$, where Ws is the stomach weight and Wt is the total weight. Although this is the most commonly used method (Elliot, Persson, 1978), limitations in the use of stomach weight should be accounted for when evaluating fish feeding dynamics (Elliasen, Jobling, 1985; Bromley, 1994). Fish stomach weight can be overestimated when prey is eaten during capture (Bromley, 1994). Inversely, stomach weight can be underestimated due to prey regurgitation during capture (Bromley, 1994), progression of digestion and evacuation in passive fishing methods, and the influence of preservation methods (Elliasen, Jobling, 1985; Bromley, 1994). In the present study, sampling occurred in different seasonal periods, and included specimens in a wide range of size classes, which can mitigate the disadvantages of the use of IR values in the estimation of *E. varii* feeding dynamics.

In order to decrease the importance of individual differences when analyzing the influence of ontogeny and seasonality in diet composition and feeding dynamics (Elliassen, Jobling, 1985), stomach contents and RI data of *E. varii* were grouped into four size classes (40 to 80 cm, 80 to 120 cm, 120 to 160 cm, and 160 to 200 cm) and two seasonal periods (rainy and dry). To analyze whether diet composition differed among size classes of electric eels and between seasonal periods, volume (Vi) of groups of prey of 28 stomachs were transformed by division by sum. The transformed data were used in the construction of a Bray-Curtis dissimilarity matrix. The latter was the basis for a Permutational Multivariate Analysis of Variance (PERMANOVA), a non-parametric statistical test that allows the investigation of differences between predefined groups (Delariva *et al*., 2013). PERMANOVA was performed with 9,999 permutations in order to test the significance of the generated values of Pseudo-F.

Electric eel size and seasonality were also tested to examine if they affected feeding dynamics through ANOVA. This analysis was based on the Stomach Repletion Index (Ri) data from 95 specimens.

Since the objective is to assess the individual effect of ontogeny and seasonality on diet and feeding dynamics, PERMANOVA and ANOVA included both factors simultaneously to eliminate any possible influence of the combined effect of the variables on the data. Probability values lower than 0.05 were considered significant. PERMANOVA and ANOVA were performed with the software R (R Core Team, 2020) using respectively the function adonis of the Vegan Package (Oksanen *et al*., 2019) and the function aov of Stats Package (R Core Team, 2020).

## RESULTS

Fishes were the most important prey (IAi = 96.66%) in the *E. varii* diet (Tab. 1). Among the fishes that could be identified, the most frequent and large were specimens of Cichlidae and Callichthyidae. Occasional consumption of crustacea (IAi = 1.45%), aquatic insects (IAi = 0.72%) and terrestrial insects (IAi = 0.78%) was observed. Electric eels had a mean IQ of 0.40±0.06.

No influence of ontogeny (PERMANOVA, pseudoF = 0.77299, p = 0.6241) and seasonality (PERMANOVA, pseudoF = 1.18292 p = 0.3024) was observed in the diet of *E. varii*. Fish were the main prey for electric eels in all size classes (Tab. 2). Fish was also the most consumed prey by *E. varii* both in the rainy and dry seasons in the Curiaú River EPA (Tab. 3).

Similar RI values were obtained for the size classes of *E. varii* (Fig. 2A), as well as

**TABLE 1 |** Preys consumed by *Electrophorus varii* in the Curiaú River EPA, state of Amapá, Brazil. Fi% = Frequency of Occurrence, Vi% = Volume and AIi% = Alimentary Index.

| Item | Fi% | Vi% | AIi% |
|---|---|---|---|
| **Fishes (Osteichthyes)** | | | |
| Fish Remains | 60.47 | 38.95 | 72.62 |
| Callichthyidae | 16.28 | 18.51 | 9.67 |
| Cichlidae | 13.95 | 19.34 | 8.66 |
| Characidae | 2.33 | 0.55 | 0.04 |
| Erythrinidae | 4.65 | 1.93 | 0.29 |
| Gymnotiformes | 4.65 | 3.87 | 0.58 |
| Synbranchidae | 4.65 | 0.55 | 0.08 |
| **Frog (Anura)** | | | |
| Hylidae | 2.33 | 1.38 | 0.10 |
| **Aquatic Insects** | | | |
| Anisoptera | 13.95 | 1.66 | 0.74 |
| Coleoptera | 2.33 | 1.66 | 0.12 |
| **Terrestrial Insects** | | | |
| Coleoptera | 2.33 | 0.83 | 0.06 |
| Hymenoptera | 2.33 | 0.28 | 0.02 |
| Insect Remains | 16.28 | 1.66 | 0.87 |
| **Crustacea** | | | |
| Shrimps (Palaemonidae) | 6.98 | 1.10 | 0.25 |
| Crabs (Tricodactylidae) | 11.63 | 5.52 | 2.06 |
| **Seeds** | | | |
| *Euterpe oleracea* | 11.63 | 2.21 | 0.83 |

**TABLE 2** | Preys consumed by size class of *Electrophorus varii* in the Curiaú River EPA, state of Amapá, Brazil. Fi% = Frequency of Occurrence, Vi% = Volume and AIi% = Alimentary Index.

| Prey/Size Class | 40–80 cm (N= 4) | | | 80–120 cm (N= 15) | | | 120–160 cm (N= 5) | | | 160–200 cm (N= 4) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Fi% | Vi% | AIi% | Fi% | Vi% | AIi% | Fi% | Vi% | AIi% | Fi% | Vi% | AIi% |
| **Fishes (Osteichthyes)** | | | | | | | | | | | | |
| Fish Remains | 75.00 | 50.00 | 70.59 | 46.67 | 22.73 | 53.68 | 100.00 | 78.00 | 94.66 | 50.00 | 44.90 | 51.16 |
| Cichlidae | | | | 6.67 | 9.09 | 3.07 | 20.00 | 4.00 | 0.97 | 50.00 | 30.61 | 34.88 |
| Callichthyidae | | | | 13.33 | 25.45 | 17.18 | | | | 25.00 | 20.41 | 11.63 |
| Characidae | | | | 6.67 | 1.82 | 0.61 | | | | | | |
| Gymnotiformes | | | | 6.67 | 9.09 | 3.07 | | | | 25.00 | 4.08 | 2.33 |
| Synbranchidae | 25.00 | 12.50 | 5.88 | 6.67 | 0.91 | 0.31 | | | | | | |
| **Frog (Anura)** | | | | | | | | | | | | |
| Hylidae | | | | 6.67 | 4.55 | 1.53 | | | | | | |
| **Aquatic Insects** | | | | | | | | | | | | |
| Anisoptera | | | | 6.67 | 0.91 | 0.31 | | | | | | |
| Coleoptera | | | | | | | 20.00 | 12.00 | 2.80 | | | |
| **Terrestrial Insects** | | | | | | | | | | | | |
| Coleoptera | | | | 6.67 | 2.73 | 0.92 | | | | | | |
| Insect Remains | 50.00 | 12.50 | 11.76 | 13.33 | 1.82 | 1.23 | | | | | | |
| **Crustacea** | | | | | | | | | | | | |
| Shrimps (Palaemonidae) | | | | 6.67 | 0.91 | 0.31 | 20.00 | 6.00 | 1.46 | | | |
| Crabs (Tricodactylidae) | | | | 20.00 | 16.36 | 16.56 | | | | | | |
| **Seeds** | | | | | | | | | | | | |
| *Euterpe oleracea* | 25.00 | 25.00 | 11.76 | 6.67 | 3.64 | 1.23 | | | | | | |

between the rainy and dry seasons (Fig. 2B). Ontogeny (ANOVA, F = 1.727, p = 0.167) and seasonality (ANOVA, F = 2.524, p = 0.116) did not influence the feeding dynamics of electric eels in the Curiaú River EPA.

## DISCUSSION

The results of the present study indicate that *E. varii* is a piscivorous predator, in disagreement with the hypothesis proposed by other authors that electric eels are generalist carnivores (Ellis, 1913; Sterba, 1959; Saul, 1975; Goulding *et al*., 1988; Planquette *et al*., 1996; Mérona, Rankin-de-Mérona, 2004; Crampton *et al*., 2013; Giora *et al*., 2014; Stoddard *et al*., 2019). The presence of açaí seeds in the stomach contents of *E. varii* was considered accidental, as it was observed in few stomachs, with only one seed per stomach, and in general seeds were accompanied by animal prey in the stomach, contrary to the hypothesis of herbivory in electric eels (Nakashima, 1941; Goulding, 1980). The lack in information on the feeding habits of these fish is probably due to the limited sample size in the few studies available (Saul, 1975; Goulding *et al*., 1988; Mérona, Rankin-de-Mérona, 2004; Crampton *et al*., 2013; Dary *et al*., 2017).

Cichlidae and Callichthydae were the most consumed groups of fishes by *E. varii*, which may be explained by their greater abundance in floodplains (Arrington,

**TABLE 3** | Preys consumed by seasonal period by *Electrophorus varii* in the Curiaú River EPA, state of Amapá, Brazil. Fi% = Frequency of Occurrence, Vi% = Volume and AIi% = Alimentary Index.

| Prey/Season | Rainy (N= 17) | | | Dry (N= 11) | | |
|---|---|---|---|---|---|---|
| | Fi% | Vi% | AIi% | Fi% | Vi% | AIi% |
| **Fishes (Osteichthyes)** | | | | | | |
| Fish Remains | 52.94 | 20.54 | 47.59 | 72.73 | 58.86 | 86.21 |
| Cichlidae | 17.65 | 35.72 | 27.59 | 9.09 | 1.27 | 0.23 |
| Callichthyidae | 5.88 | 7.14 | 1.84 | 18.18 | 25.32 | 9.27 |
| Characidae | 5.88 | 1.79 | 0.46 | | | |
| Gymnotiformes | | | | 18.18 | 8.86 | 3.24 |
| Synbranchidae | 11.76 | 1.79 | 0.92 | | | |
| **Frog (Anura)** | | | | | | |
| Hylidae | 5.88 | 4.46 | 1.15 | | | |
| **Aquatic Insects** | | | | | | |
| Anisoptera | 5.88 | 0.89 | 0.23 | | | |
| Coleoptera | | | | 9.09 | 3.80 | 0.70 |
| **Terrestrial Insects** | | | | | | |
| Coleoptera | 5.88 | 2.68 | 0.69 | | | |
| Insect Remains | 23.53 | 2.68 | 2.76 | | | |
| **Crustacea** | | | | | | |
| Shrimps (Palaemonidae) | 5.88 | 0.89 | 0.23 | 9.09 | 1.90 | 0.35 |
| Crabs (Tricodactylidae) | 17.65 | 16.07 | 12.41 | | | |
| **Seeds** | | | | | | |
| *Euterpe oleracea* | 17.65 | 5.36 | 4.14 | | | |

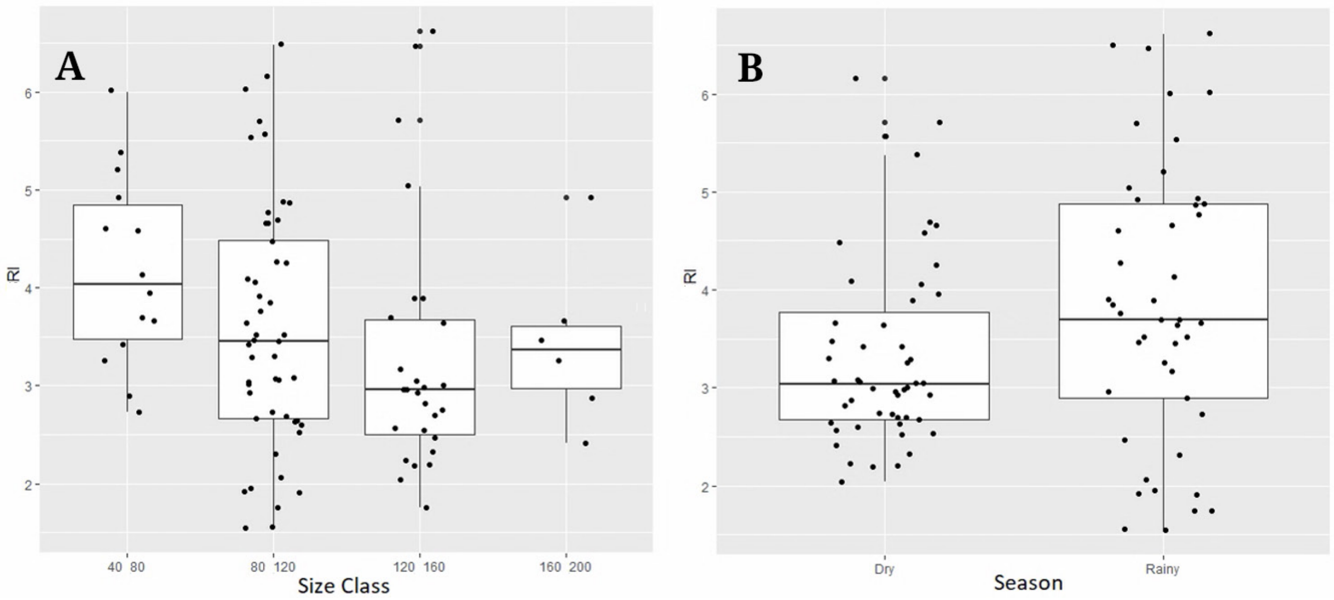


**FIGURE 2** | Variation in Stomach Repletion Index (RI) values (black spots) of *Electrophorus varii* in Curiaú River EPA Amapá, Brazil. **A.** Size class; and **B.** Season. The lower and upper bars of the boxplot represent 25 and 75 quartiles, respectively. The horizontal bar within each boxplot represents the mean RI value. The lower and upper vertical line represent the RI values amplitude.

Winemiller, 2006; Albuquerque, Barthem, 2008), particularly in the Curiaú River EPA (Chellappa *et al*., 2005). Ingestion of prey with anti-predation morphological adaptations, such as fin spines of Cichlidae and lateral dermal plates of Callichthyidae (Kirchheim, Goulart, 2010), reflects the efficacy of predatory tactics of electric eels, such as "Remote Control" described by Catania (2014). In addition to strong electrical discharges, electric eels breathe air (Johansen *et al*., 1968), allowing them to access shallow and anoxic areas commonly used as a refuge by small prey (Anjos *et al*., 2008), and consumption of preys with morpho-physiological adaptations to water with low dissolved oxygen concentrations such as Callichthyidae fish (Brauner *et al*., 1995). Some electric fish were found in the stomach content of *E. varii* in the Curiaú River EPA, which was also observed in nature and experiments in the laboratory (Bullock *et al*., 1979; Westby, 1988; Stoddard, 1999). However, considering its low importance in the *E. varii* diet, as suggested by Stoddard *et al.* (2019), electric eels cannot be considered as predators specialized in electric fish (Stoddard, 1999; Moyle, Cech Jr, 2004).

Fishes were the main preys of electric eels regardless of size class or seasonal period, reinforcing that piscivory is the main feeding habit of *E. varii* in the Curiaú River EPA. However, there was very occasional consumption of arthropods in most size classes and in the rainy and dry seasons. The sporadic consumption of arthropods by piscivorous predators, such as electric eels, is not surprising (Luz-Agostinho *et al*., 2008), since plasticity and trophic opportunism in the consumption of prey are common characteristics of freshwater fishes (Abelha *et al*., 2001), especially in floodplains with seasonal changes in food availability and quality (Junk *et al*., 1997; Mortillaro *et al*., 2015). Predation of amphibians and small mammals has also been reported in *E. electricus* in French Guiana (Planquette *et al*., 1996) and in a sample of *E. voltai* in the Jari River, Brazil (Oliveira *et al*., 2019), but the presence of a frog in a single stomach in the present study suggests that predation of small vertebrates by *E. varii* in the wild is unusual.

Electric eels with sizes between 40 and 178 cm have a fish-eating habit. Because the mean size of the first gonadal maturation of *E. varii* is 85 cm (Mendes-Júnior *et al*., 2016), young individuals larger than 40 cm and adults of *E. varii* can be considered fish predators. However, the influence of ontogeny in the diet of electric eels can not be ruled out, given that in Ilha do Marajó, *E. varii* with total length up to 8 cm consumed mainly conspecific eggs and embryos (cannibalism), followed by the replacement of these preys with crustacean larvae by 9 cm electric eels (Assunção, Schwassmann, 1995). This suggests that ontogenetic changes in the diet of *E. varii* of sizes ranging between 10 to 40 cm can occur.

The absence of effect of seasonality on the diet of electric eels may be due to the predominance of fish consumption in both rainy and dry seasons, as electric eels are predatory piscivorous regardless of the time of year. Fish in river-floodplain systems are generally more easily caught during the dry season, when water bodies retract and preys are confined in the river channel and in marginal residual pools. Comparatively, in the rainy season, the flooding of extensive land areas due to rains promotes the dispersion of fish in the floodplain (Junk *et al*., 1997), forcing piscivorous predators to modify their diets according to the seasonal period (Lowe-McConnell, 1999; Luz-Agostinho *et al*., 2008). The varied hunting tactics of electric eels (Catania, 2019) allow them to locate fish, their main prey, dispersed in the floodplain in the rainy season as well as confined to residual pools during the drought, which would explain the absence of effect of seasonality on the diet of *E. varii*.

Considering that the ratio between intestine size and fish size reflects their eating habits, ranging from short intestines of carnivores to long-intestines of herbivores, and intermediate-sized intestines of omnivores (Fryer, Iles, 1972; Barbieri *et al*., 1994; Gerking, 1994; Ward-Campbell *et al*., 2005), the short intestine of electric eels reflects their carnivorous eating habits. The average IQ of *E. varii* is short when compared to that of the piscivore *Hoplias malabaricus* (Bloch, 1794), with IQ values above 0.53 (Mazzoni, Costa, 2007; Peretti, Andrian, 2008), but the small visceral cavity in relation to the body size of Gymnotiformes do not allow a comparison of IQ values of this group with those of other Teleostei fish. The mean IQ of *E. varii* is lower than the IQ of the generalist carnivore *Sternopygus macrurus* (Bloch & Schneider, 1801) (IQ = 0.60) (Olaya-Nieto *et al*., 2009) and is higher than that observed in invertivorous electric fish such as *Eigenmannia trilineata* López & Castello, 1966 (IQ = 0.25), *Brachyhypopomus bombilla* Loureiro & Silva, 2006 (IQ = 0.27), and *Brachyhypopomus gauderio* Giora & Malabarba, 2009 (IQ = 0.29) (Peretti, Adrian, 1999; Giora *et al*., 2012; Giora *et al*., 2014), which contradicts the idea that the IQ of fish-eating predators tends to be lower than that of invertivores. The values observed in *E. varii* might be higher due to its larger body cavity (covering more than 30 vertebrae) compared to the 16 to 19 vertebrae in *Brachyhypopomus* Mago-Leccia, 1994 and *Eigenmannia* Jordan & Evermann, 1896 (Peixoto *et al*., 2015; Crampton *et al*., 2016). If the intestine is a good indicator of the diet of electric fish, and since *Gymnotus*, the putative sister group of *Electrophorus* (*e.g.* Alda *et al*., 2019), consists of voracious predators of fish and insects (Campos-da-Paz, 2003), their intestine is likely intermediate in length between the ones observed in *Electrophorus* (IQ = 0.40) and those documented in *Eigenmannia* and *Brachyhypopomus* species (IQ = 0.25).

Similar to the observed for diet composition, the feeding dynamics of *E. varii* did not differ among size classes and between seasonal periods in the Curiaú River EPA, which may reflect the high capacity of electric eels to locate and subdue prey using weak and strong electrical discharges, respectively. The electrical organ of *E. varii* individuals with a length of at least 40 cm can produce discharges greater than 300 volts (from de Santana *et al*., 2019), thus, electric eels of all size classes analyzed in the present study were equally lethal to prey fish. In addition, the hunting tactics of electric eels described by Catania (2019) allow them to find and control mobile or sedentary prey, regardless of the time of year. Visually oriented piscivorous predators, such as species of *Hydrolycus* Müller & Troschel, 1844, have different feeding dynamics than those observed in electric eels. They modify their feeding activity according to the seasonal period (Barbosa *et al*., 2018), since the flooding of river banks in the rainy season provides new refuges for prey, making it difficult for predators to hunt (Lowe-McConnell, 1999), which probably does not occur with *E. varii*. The present study reports the initial findings of the feeding dynamics of electric eels, due to limitations in the use of stomach weight to measure feeding activity in fishes species (Elliasen, Jobling, 1985; Bromley, 1994).

In conclusion, our findings reveal that electric eels are piscivorous predators and that fishes are the main prey of young individuals (Lt 45–85 cm) and adults (Lt > 85 cm), regardless of the time of year. Future analyzes of the stomach contents of 10–40 cm individuals may indicate in what size class there is a change from a diet rich in crustacean larvae (Assunção, Schwassmann, 1995) to a piscivorous diet (present study). Our initial findings also indicate that the feeding dynamics of electric eels are not influenced by ontogeny and seasonality. However, future studies with more robust methods than the analysis of stomach weight are needed to more effectively measure the feeding dynamics of electric eels. Protection and management strategies and actions are essential to ensure that future generations can experience the celebrate electric eel not only in zoos, public aquariums, wildlife books and documentaries, but in their natural habitat.

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## REFERENCES


- **Abelha MCF, Agostinho AA, Goulart E.** Plasticidade trófica em peixes de água doce. Acta Sci. 2001; 23(2):425–34. http://ftp.nupelia.uem.br/users/agostinhoaa/publications/105-AC-Abelha-et-al.pdf
- **Albert JS**. Species Diversity and phylogenetic systematics of American Knifefishes (Gymnotiformes, Teleostei). Ann Arbor, Michigan: The University of Michigan. 2001.
- **Albuquerque AAD, Barthem RB**. A pesca do tamoatá *Hoplosternum littorale* (Hancock, 1828) (Siluriformes: Callichthyidae) na ilha de Marajó. Bol. Mus Para Emílio Goeldi Cienc Hum. 2008; 3(3):359–72. http://dx.doi.org/10.1590/S1981-81222008000300006
- **Alda F, Tagliacollo VA, Bernt MJ, Waltz BT, Ludt WB, Faircloth BC, Alfaro ME, Albert JS, Chakrabarty P**. Resolving deep nodes in an ancient radiation of neotropical fishes in the presence of conflicting signals from incomplete lineage sorting. Syst Biol. 2019; 68(4):573–93. http://dx.doi.org/10.1093/sysbio/syy085
- **Anjos MB, De Oliveira RR, Zuanon J**. Hypoxic environments as refuge against predatory fish in the Amazonian floodplains. Braz J Biol. 2008; 68(1):45–50. http://dx.doi.org/10.1590/S1519-69842008000100007
- **Arrington DA, Winemiller KO**. Habitat affinity, the seasonal flood pulse, and community assembly in the littoral zone of a Neotropical floodplain river. J North Am Benthol Soc. 2006; 25(1):126–41. http://dx.doi.org/10.1899/0887-3593(2006)25%5B126:HATSFP%5D2.0.CO;2
- **Assunção MIS, Schwassmann HO**. Reproduction and larval development of *Electrophorus electricus*on Marajó Island (Pará, Brazil). Ichthyol Explor Fres. 1995; 6:175–84.
- **Barbieri G, Barbieri MC**. Note on nutritional dynamics of *Gymnotus carapo* (L.) from the Lobo reservoir, São Paulo State, Brazil. J Fish Biol. 1984; 24(4):351–55. http://dx.doi.org/10.1111/j.1095-8649.1984.tb04807.x

- **Barbieri G, Peret AC, Verani JR**. Notas sobre a adaptação do trato digestivo ao regime alimentar em espécies de peixes da região de São Carlos (SP). I. Quociente intestinal. Rev Bras Biol. 1994; 54:63–69.
- **Barbosa TA, Rosa DC, Soares BE, Costa CH, Esposito MC, Montag LF**. Effect of flood pulses on the trophic ecology of four piscivorous fishes from the eastern Amazon. J Fish Biol. 2018; 93(1):30–39. http://dx.doi.org/10.1111/jfb.13669
- **Bauer R**. Electric organ discharge (EOD) and food items capture behaviour in the electric eel, *Electrophorus electricus*. Behav Ecol Sociobiol. 1979; 4:311–19. https://doi.org/10.1007/BF00303239
- **Bowen SH**. Detritivory in neotropical fish communities. Environ Biol Fishes. 1983; 9:137–44. http://dx.doi.org/10.1007/BF00690858
- **Brauner CJ, Ballantyne CL, Randall DJ, Val AL**. Air breathing in the armoured catfish (*Hoplosternum littorale*) as an adaptation to hypoxic, acidic, and hydrogen sulphide rich waters. Can J Zool. 1995; 73(4):739–44. http://dx.doi.org/10.1139/z95-086
- **Bromley PJ**. The role of gastric evacuation experiments in quantifying the feeding rates of predatory fish. Rev Fish Biol Fish. 1994; 4:36–66. http://dx.doi.org/10.1007/BF00043260
- **Bullock TH, Fernandes-Souza N, Graf W, Heiligenberg W, Langner G, Meyer DL, Pimentel-Souza M F, Scheich H, Viancour TA**. Aspectos do uso da descarga do órgão elétrico e eletrorrecepção nos Gymnotoidei e outros peixes amazônicos. Acta Amazon. 1979; 9(3):549–72. http://dx.doi.org/10.1590/1809-43921979093549
- **Campos-da-Paz R**. Family Gymnotidae. In: Reis RE, Kullander SO, Ferraris CJ, Jr., organizers. Check list of the freshwater fishes of South and Central America. Porto Alegre: Edipucrs; 2003. p.483–86.
- **Cardoso DC, deHart P, Freitas CEDC, Siqueira-Souza FK**. Dieta e ecomorfologia de peixes predadores em lagos de várzea da Amazônia. Biota Neotrop. 2019; 19(3):e20180678. https://doi.org/10.1590/1676-0611-bn-2018-0678
- **Catania K**. The shocking predatory strike of the electric eel. Science. 2014; 346(6214):1231–34. http://dx.doi.org/10.1126/science.1260807
- **Catania KC**. The astonishing behavior of electric eels. Front Integr Neurosc. 2019; 13:23. http://dx.doi.org/10.3389/fnint.2019.00023
- **Chellappa S, Sá-Oliveira JC, Chellappa NT**. Fish fauna of a temporary lake in an Amazonian Conservation Area. Acta Limnol Bras. 2005; 17(3):283–89.
- **Crampton WGR**. Gymnotiform fish: an important component of Amazonian floodplain fish communities. J Fish Biol. 1996; 48(2):298–301. https://doi.org/10.1111/j.1095-8649.1996.tb01122.x
- **Crampton WG, Lovejoy NR, Waddell JC**. Reproductive character displacement and signal ontogeny in a sympatric assemblage of electric fish. Evolution. 2011; 65(6):1650–66. http://dx.doi.org/10.1111/j.1558-5646.2011.01245.x
- **Crampton WGR, Ribeiro AC**. Gymnotidae. In: Queiroz LJ, Torrente-Vilara G, Ohara WM, Pires THS, Zuanon J, Doria CRC, editors. Peixes do Rio Madeira Volume III. São Paulo: São Paulo Energia; 2013. p.207–17.
- **Crampton WG, de Santana CD, Waddell JC, Lovejoy NR**. A taxonomic revision of the Neotropical electric fish genus *Brachyhypopomus* (Ostariophysi: Gymnotiformes: Hypopomidae), with descriptions of 15 new species. Neotrop Ichthyol. 2016; 14(4):639–790. http://dx.doi.org/10.1590/1982-0224-20150146
- **Crampton WGR, Wells JK, Smyth C, Walz SA**. Design and construction of an electric fish finder. Neotrop Ichthyol. 2007; 5(3):425–28. http://dx.doi.org/10.1590/S1679-62252007000300022
- **Dary EP, Ferreira E, Zuanon J, Röpke CP**. Diet and trophic structure of the fish assemblage in the mid-course of the Teles Pires River, Tapajós River basin, Brazil. Neotrop Ichthyol. 2017; 15(4):e160173. http://dx.doi.org/10.1590/1982-0224-20160173
- **Delariva RL, Hahn NS, Kashiwaqui EAL**. Diet and trophic structure of the fish fauna in a subtropical ecosystem: impoundment effects. Neotrop Ichthyol. 2013; 11:891-904. https://doi.org/10.1590/S1679-62252013000400017
- **Eliassen JE, Jobling M**. Food of the roughhead grenadier, *Macrourus berglax*, Lacepede in North Norwegian waters. J Fish Biol. 1985; 26(3):367–76. http://dx.doi.org/10.1111/j.1095-8649.1985.tb04276.x

- **Ellis MM**. The gymnotid eels of tropical America. Mem Carnegie Mus. 1913; 6(3):109–95.
- **Elliott JM, Persson L**. The estimation of daily rates of food consumption for fish. J Anim Ecol. 1978; 47(3):977–91. http://dx.doi.org/10.2307/3682
- **Ferraris CJ Jr., de Santana CD, Vari RP**. Checklist of Gymnotiformes (Osteichthyes: Ostariophysi) and catalogue of primary types. Neotrop Ichthyol. 2017; 15(1):e160067. http://dx.doi.org/10.1590/1982-0224-20160067
- **Ferriz RA, Iwaszkiw JM**. Alimentación de *Gymnotus omarorum* (Gymnotiformes: Gymnotidae) em Laguna Blanca (Parque Nacional Río Pilcomayo), Formosa, Argentina. Rev Mus Argentino Cienc Nat. 2014; 16(2):115–22. Available from: http://hdl.handle.net/11336/19132
- **Fryer G, Iles TD**. The cichlid fishes of the great lakes of Africa, their biology and distribution. Edinburgh: Oliver and Boyd; 1972.
- **Gama CS, Halboth DA**. Ictiofauna das ressacas das bacias do Igarapé da Fortaleza e do Rio Curiaú. In: Takiyama LR, Silva AQ, editors. Diagnóstico das ressacas do estado do Amapá: bacias do Igarapé da Fortaleza e Rio Curiaú, Macapá-AP. Macapá: CPAQ/IEPA and DGEO/SEMA; 2003. p.23–52.
- **Gerking SD**. Feeding ecology of fish. London: Academic Press; 1994.
- **Giora J, Fialho CB, Dufech APS**. Feeding habit of *Eigenmannia trilineata* Lopez & Castello, 1966 (Teleostei: Sternopygidae) of Parque Estadual de Itapuã, RS, Brazil. Neotrop Ichthyol. 2005; 3(2):291–98. http://dx.doi.org/10.1590/S1679-62252005000200007
- **Giora J, Tarasconi HM, Fialho CB**. Reproduction and feeding habits of the highly seasonal *Brachyhypopomus bombilla* (Gymnotiformes: Hypopomidae) from southern Brazil with evidence for a dormancy period. Environ Biol Fishes. 2012; 94:649–62. http://dx.doi.org/10.1007/s10641-011-9971-3
- **Giora J, Tarasconi HM, Fialho CB**. Reproduction and feeding of the electric fish *Brachyhypopomus gauderio* (Gymnotiformes: Hypopomidae) and the discussion of a life history pattern for gymnotiforms from high latitudes. PloS One. 2014; 9(9):e106515. http://dx.doi.org/10.1371/journal.pone.0106515
- **Goulding M**. The fishes and the forest: explorations in Amazonian natural history. California: Univ of California Press; 1980.
- **Goulding M, Carvalho ML, Ferreira EJG**. Rio Negro, rich life in poor water. The Hague: SPB Academic Publishing; 1988.
- **Griffiths SP, Kuhnert PM, Fry GF, Manson FJ**. Temporal and size-related variation in the diet, consumption rate, and daily ration of mackerel tuna (*Euthynnus affinis*) in neritic waters of eastern Australia. ICES J Mar Sci. 2009; 66(4):720–33. http://dx.doi.org/10.1093/icesjms/fsp065
- **Hahn NS, Almeida VLL, Luz KDG**. Alimentação e ciclo alimentar diário de *Hoplosternum littorale* (Hancock) (Siluriformes, Callichthyidae) nas lagoas Guaraná e Patos da planície do alto Paraná, Brasil. Rev Bras Zool. 1997; 14(1):57–64. http://dx.doi.org/10.1590/S0101-81751997000100005
- **Hunter J**. An Account of the *Gymnotus electricus*. By John Hunter FRS. Philos Trans. 1775; 65:395–407. Available from: https://www.jstor.org/stable/106210
- **Hynes HBN**. The food of fresh-water sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*), with a review of methods used in studies of the food of fishes. J Anim Ecol. 1950; 19(1):36–58. http://dx.doi.org/10.2307/1570
- **Hyslop EJ**. Stomach contents analysis – a review of methods and their application. J Fish Biol. 1980; 17(4):411–29. http://dx.doi.org/10.1111/j.1095-8649.1980.tb02775.x
- **Johansen K, Lenfant C, Schmidt-Nielsen K, Petersen JA**. Gas exchange and control of breathing in the electric eel, *Electrophorus electricus*. Z Vgl Physiol. 1968; 61:137–63. http://dx.doi.org/10.1007/BF00341112
- **Junk WJ, Soares MGM, Saint-Paul U**. The fish. In: Junk WJ, editor. The Central Amazon Floodplain: ecology of a pulsing system. Berlin: Springer-Verlag; 1997. p.385–408.
- **Kawakami E, Vazzoler G**. Método gráfico e estimativa de índice alimentar aplicado no estudo de alimentação de peixes. Bol Inst Oceanogr. 1980; 29: 205-207.
- **Kirchheim PD, Goulart E**. Ecomorphology of predation and antipredation in Siluriformes (Osteichthyes). Oecologia Australis. 2010; 14:550–68.

- **Lima-Junior SE, Goitein R**. A new method for the analysis of fish stomach contents. Acta Sci. 2001; 23(2):421–24.
- **Lowe-McConnell RH**. Estudos ecológicos de comunidades de peixes tropicais. São Paulo: Edusp; 1999.
- **Luz-Agostinho KD, Agostinho AA, Gomes LC, Júlio HF**. Influence of flood pulses on diet composition and trophic relationships among piscivorous fish in the upper Paraná River floodplain. Hydrobiologia. 2008; 607:187–98. http://dx.doi.org/10.1007/s10750-008-9390-4
- **Mago-Leccia F**. Electric fishes of the continental waters of America: classification and catalogue of the electric fishes of the order Gymnotiformes (Teleostei: Ostariophysi), with descriptions of new genera and species. Caracas: Fundacion para Desarrollo de las Ciencias Fiscias, Matematicas y Naturales; 1994.
- **Mazzoni R, Costa LDSD**. Feeding ecology of stream-dwelling fishes from a coastal stream in the Southeast of Brazil. Braz Arch Biol Technol. 2007; 50(4):627–35. http://dx.doi.org/10.1590/S1516-89132007000400008
- **Mendes-Junior RNG, Sá-Oliveira JC, Ferrari S**. Biology of the Electric Eel *Electrophorus electricus* Linnaeus. 1766 (Gymnotiformes: Gymnotidae) on the floodplain of the Curiaú River. eastern Amazonia. Rev Fish Biol Fish. 2016; 26:83–91. http://dx.doi.org/10.1007/s11160-015-9407-9
- **Mérona B, Rankin-de-Mérona J**. Food resource partitioning in a fish community of the central Amazon floodplain. Neotrop Ichthyol. 2004; 2(2):75–84. http://dx.doi.org/10.1590/S1679-62252004000200004
- **Moller P**. Electric fishes: history and behavior (Vol. 17). New York: Springer; 1995.
- **Mortillaro JM, Pouilly M, Wach M, Freitas CEC, Abril G, Meziane T**. Trophic opportunism of central Amazon floodplain fish. Freshwater Biology. 2015; 60(8):1659–70. http://dx.doi.org/10.1111/fwb.12598
- **Moyle PB, Cech Jr JJ**. Fishes: an introduction to ichthyology. New Jersey: Pearson Prentice Hall; 2004.
- **Nakashima S**. Una nueva especie de anguila eléctrica del Perú. Boletín del Museo de Historia Natural “Javier Prado”. 1941; 5:461–65.
- **Novaes JLC, Caramaschi EP, Winemiller KO**. Feeding of *Cichla monoculus* Spix, 1829 (Teleostei: Cichlidae) during and after reservoir formation in the Tocantins River, Central Brazil. Acta Limnol Bras. 2004; 16(1):41–49.
- **Olaya-Nieto C, Soto-Fernández P, Barrera-Chica J**. Feeding habits of Mayupa (*Sternopygus macrurus* Bloch & Schneider, 1801) in the Sinu River, Colombia. Revista MVZ Córdoba. 2009; 14:1787–95.
- **Oliveira MSB, Esteves-Silva PH, Santos-Jr AP, Kawashita-Ribeiro RA, Tavares-Dias M**. Predation on *Typhlonectes compressicauda* (Duméril & Bibron, 1841) (Gymnophiona: Typhlonectidae) by *Electrophorus voltai* de Santana *et al*., 2019 (Pisces: Gymnotidae) and a new distributional record in the Amazon basin. Herpetol Notes. 2019; 12:1141–43.
- **Oksanen J, Guillaume Blanchet F, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O’Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H**. Vegan: Community Ecology Package. R package version 2.5-6. 2019. Available from: https://CRAN.R-project.org/package=vegan
- **Peixoto LAW, Dutra GM, Wosiacki WB**. The electric glass knifefishes of the *Eigenmannia trilineata* species-group (Gymnotiformes: Sternopygidae): monophyly and description of seven new species. Zool J Linnean Soc. 2015; 175(2):384–414. https://doi.org/10.1111/zoj.12274
- **Pereira LS, Agostinho AA, Delariva RL**. Effects of river damming in Neotropical piscivorous and omnivorous fish: feeding, body condition and abundances. Neotrop Ichthyol. 2016; 14(1):e150044. http://dx.doi.org/10.1590/1982-0224-20150044
- **Peretti D, Andrian IDF**. Feeding of *Eigenmannia trilineata* (Pisces, Sternopygidae) (Lopez & Castello, 1966), in the upper Paraná River floodplain, Brazil. Braz Arch Biol Technol. 1999; 42(1):00–00. http://dx.doi.org/10.1590/S1516-89131999000100011
- **Peretti D, Andrian IDF**. Feeding and morphological analysis of the digestive tract of four species of fish (*Astyanax altiparanae*, *Parauchenipterus galeatus*, *Serrasalmus marginatus* and *Hoplias* aff. *malabaricus*) from the upper Paraná River floodplain, Brazil. Braz J Biol. 2008; 68(3):671–79. http://dx.doi.org/10.1590/S1519-69842008000300027

- **Planquette P, Keith P, Le Bail P**. Atlas des poissons d'eau douce de Guyane. French Guyana: INRA; 1996.
- **R Development Core Team**. R: a language and environment for statistical computing [Computer software manual - Internet]. Vienna: R Foundation for Statistical Computing; 2020. Available from: https://www.r-project.org/
- **Sachs K, Fritsch GT**. Untersuchungen am Zitteraal: *Gymnotus electricus*. Leipzig: Veit; 1881.
- **Sá-Oliveira JC, Angelini R, Isaac-Nahum VJ**. Diet and niche breadth and overlap in fish communities within the area affected by an Amazonian reservoir (Amapá, Brazil). An Acad Bras Cienc. 2014; 86(1):383–405. http://dx.doi.org/10.1590/0001-3765201420130053
- **Sá-Oliveira JC, Mendes-Junior RNG**. Fecundidade e tipo de desova do poraquê, *Electrophorus electricus* (Lineus, 1766) (Osteichhyes: Gymnotiformes: Gymnotidae) da Área de Proteção Ambiental–APA–do Rio Curiaú, Macapá-AP. Biota Amaz. 2012; 2(1):32–36. http://dx.doi.org/10.18561/2179-5746/biotaamazonia.v2n1p32-36
- **de Santana CD, Crampton WG, Dillman CB, Frederico RG, Sabaj MH, Covain R, Ready J, Zuanon J, Oliveira RR, Mendes-Júnior RNG, Bastos DA, Teixeira TF, Mol J, Ohara W, Castro NC, Peixoto LA, Nagamachi C, Sousa L, Montag LFA, Ribeiro F, Waddell JC, Piorsky NM, Vari RP, Wosiacki WB**. Unexpected species diversity in electric eels with a description of the strongest living bioelectricity generator. Nat Commun. 2019; 10:4000. http://dx.doi.org/10.1038/s41467-019-11690-z
- **Santos EP**. Dinâmica de populações aplicada à pesca e piscicultura. São Paulo: Hucitec/Edusp; 1978.
- **Saul WG**. An ecological study of fishes at a site in upper Amazonian Ecuador. Proc Acad Nat Sci Philadelphia. 1975; 127:93–134. Available from: https://www.jstor.org/stable/4064705
- **Soares MGM, Almeida RG, Junk WJ**. The trophic status of the fish fauna in Lago Camaleao a macrophyte dominated floodplain lake in the middle Amazon. Amazoniana. 1986; 9(4):511–26.
- **Sterba G**. Freshwater fishes of the world. London:Vista Books; 1959.
- **Stoddard PK**. Predation enhances complexity in the evolution of electric fish signals. Nature. 1999; 400:254 –56. http://dx.doi.org/10.1038/22301
- **Stoddard PK, Tran A, Krahe R**. Predation and crypsis in the evolution of electric signaling in weakly electric fishes. Front Ecol Evol. 2019, 7:264. http://dx.doi.org/10.3389/fevo.2019.00264
- **Val AL, Silva MNP, Almeida-Val VMF**. Hypoxia adaptation in fish of the Amazon: a never-ending task. S Afr J Zool. 1998; 33(2):107–14. http://dx.doi.org/10.1080/02541858.1998.11448459
- **Ward-Campbell BMS, Beamish FWH, Kongchaiya C**. Morphological characteristics in relation to diet in five coexisting Thai fish species. J Fish Biol. 2005; 67(5):1266–79. http://dx.doi.org/10.1111/j.1095-8649.2005.00821.x
- **Westby GWM**. The ecology discharge diversity and predatory behaviour of gymnotiforme electric fish in the coastal streams of French Guiana. Behav Ecol Sociobiol. 1988; 22:341–54. https://link.springer.com/article/10.1007/BF00295103#citeas
- **Williamson HX**. Experiments and observations on the *Gymnotus electricus*, or electric eel. Phil Trans. 1775; 65:94–101. https://doi.org/10.1098/rstl.1775.0011
- **Winemiller KO**. Ontogenetic diet shifts and resource partitioning among piscivorous fishes in the Venezuelan llanos. Environ Biol Fishes. 1989; 26:177–99.


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**Raimundo Nonato Gomes Mendes-Júnior:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing-original draft, Writing-review & editing.

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## COMPETING INTERESTS

The authors declare no competing interests.

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