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Distribution, feeding and ecomorphology of four species of Auchenipteridae (Teleostei: Siluriformes) in Eastern Amazonia, Brazil

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ABSTRACT. Fish exhibit morphological, physiological and behavioral specializations which enable them to display different ways to explore the environments and resources. Thus, the aim of this study was to verify how four Auchenipteridae species differ in the distribution, feeding habits and morphological traits: *Auchenipterichthys longimanus* (Günther, 1864), *Auchenipterus nuchalis* (Spix & Agassiz, 1829), *Tatia intermedia* (Steindachner, 1877) and *Trachelyopterus galeatus* (Linnaeus, 1766). This study was conducted in rivers and bays of the Anapú Basin, Pará State (Brazil), where these species are abundant. Specimens were collected using gillnets, and after caught the stomachs were removed for the contents analyzes. Eighteen morphometric measurements from ten adult specimens of each species were taken, combined into fifteen ecomorphological attributes. The species distribution showed that *A. longimanus* was restricted to rivers, while the others were exclusively caught in the bays. All four species had their diet composed of allochthonous insects, but *A. longimanus* also exhibited a great frugivorous habit. The most important ecomorphological attributes were relative to the consumption of larger food items (for *A. longimanus* and *T. galeatus*) and to the longer swimming capacity (for *A. longimanus* and *T. intermedia*). These morphological differences and the trophic diversity presented in this study highlighted some important information about how ecomorphological similar species behave and share resources, which may play a significant role on the coexistence of these species in the Anapú Basin.

KEYWORDS. Fish, morphology, diet, adaptation.

RESUMO. Distribuição, alimentação e ecomorfologia de quarto espécies de Auchenipteridae (Teleostei: Siluriformes) da Amazônia Oriental, Brasil. Peixes apresentam especializações morfológicas, fisiológicas e comportamentais que permite a exploração do ambiente e dos recursos de diferentes maneiras. Sendo assim, o objetivo deste trabalho foi verificar como quatro espécies de peixes da Família Auchenipteridae diferem quanto à distribuição, alimentação e traços morfológicos: *Auchenipterichthys longimanus* (Günther, 1864), *Auchenipterus nuchalis* (Spix & Agassiz, 1829), *Tatia intermedia* (Steindachner, 1877) e *Trachelyopterus galeatus* (Linnaeus, 1766). Esse estudo foi realizado nos rios e baías da Bacia do Rio Anapú, Estado do Pará (Brasil), onde essas espécies são abundantes. Os espécimes foram coletados com rede de espera, e após a captura os estômagos foram removidos para a análise dos conteúdos. Dezoito medidas morfométricas foram aferidas de dez indivíduos adultos de cada espécie, posteriormente combinadas em quinze atributos ecomorfológicos. A distribuição das espécies evidenciou que *A. longimanus* foi restrita aos ambientes de rios, enquanto as demais foram exclusivamente capturadas nas baías. Todas as quatro espécies tiveram a dieta composta por insetos alóctones, mas *A. longimanus* também apresentou hábito frugívoro. Os mais importantes atributos ecomorfológicos foram relativos ao consumo de itens alimentares grandes (para *A. longimanus* e *T. galeatus*) e a maior capacidade natatória (para *A. longimanus* e *T. intermedia*). Essas diferenças morfológicas e a diversidade trófica apresentada neste estudo elucidam importantes informações sobre como espécies ecomorfologicamente semelhantes compartilham os recursos, desempenhando um papel significativo na coexistência dessas espécies na bacia do Rio Anapú.

PALAVRAS-CHAVE. Peixe, morfologia, dieta, adaptação.

Fish have different morphological, physiological and behavioral specializations that enable them to show a great plasticity in the resource and habitat usage (Lowe-McConnell, 1987). The knowledge of fish diet is an important way to understand the relationships between the species and the environment in which they live, considering both biological and ecological aspects (Moreira & Zuanon, 2002; Ramírez *et al*., 2015).

Several studies focusing on feeding biology have been conducted in natural communities of freshwater fish in Brazil, through a detailed investigation of the feeding habits as an alternative way to analyze the use of habitat by different species (Baker *et al*., 2014). Indirect methods, as ecomorphology, were also used for the description of the feeding and environmental tactics of the species (Winemiller, 1991; Severo-Neto *et al*., 2015).

Ecomorphology is included in the evolutionary biology, and is used to describe relationships between morphology and ecology by studying the relationship between body shape and organisms' ecological features (Gatz Jr., 1979; Watson & Balon, 1984; Winemiller, 1991). It is based on the idea that the morphological differences between species are caused by the pressure of different types of environments (Beaumord & Petrere Jr., 1994). Thus, significant relationships between morphology and ecology can occur due to the phylogenetic proximity. Phylogenetic information within ecomorphological analyses is the only way to objectively identify cases of morphological and adaptive convergence and divergence (Casatti & Castro, 2006). Essentially, this integration allows the better comprehension of evolutionary patterns within the communities (Peres-Neto, 1999).

Regarding the Family Auchenipteridae (Siluriformes), available data on ecology and biology addresses only a few species (Moresco & Bemvenuti, 2005; Santos, 2005; Freitas *et al*. 2011; Maia *et al*., 2013; Santos *et al*., 2013). The Auchenipteridae species are endemic to the Neotropics and belong to two subfamilies: Centromochlinae and Auchenipterinae (Birindelli, 2014).

This study was conducted in rivers of Caxiuanã National Forest in the Anapú Basin, Pará State (Brazil), where four Auchenipteridae species were abundant (Montag *et al*., 2013): *Auchenipterichthys longimanus* (Günther, 1864), *Auchenipterus nuchalis* (Spix & Agassiz, 1829), *Trachelyopterus galeatus* (Linnaeus, 1766) (belong to the Auchenipterinae group) and *Tatia intermedia* (Steindachner, 1877) (Centromochlinae group). The Auchenipteridae species are generalized as carnivorous, preying mainly insects as well plankton and fish (Ferraris Jr., 2003). Thus, the aim of this study was to verify the distribution, feeding habits and morphological traits of these species, in an attempt to verify how closely related species differ in the use of resources.

MATERIAL AND METHODS

Study area. Caxiuanã National Forest (FLONA of Caxiuanã) is located downstream from the Anapu River, between Tocantins and Xingu rivers, eastern Amazonia, in the municipalities of Melgaço and Portel (State of Pará, Brazil) (Fig. 1). The main water systems of the Caxiuanã region are rivers and bays. The rivers are narrower and deeper than the bays, with vegetation limited to the river edge and sporadic floating macrophyte banks. The bays are marked by areas that have a greater width and lower depth with a high frequency of large floating macrophyte banks, mainly *Eicchornia* spp. and *Cyperacea* (Montag *et al*., 2008). The bays are "rias fluviais" formed by fractures that have been enlarged by sediment deposited into their mouths, forming natural underwater dams which transform them into "lakes". Additionally, a complex network of rivers and streams create an extremely heterogeneous environment (Costa *et al*., 2002).

Data sampling. Specimens were collected in March/April 2004 (high-water period) and October/November 2004 (low-water period), 40 days per period, using gill nets of 80 m long, with different mesh sizes. The nets were set up at midnight and removed in the next morning, between 07 h and 08 h. The sites where the nets were set up were selected with the help of a local fisherman, who pointed out the best areas for possible catches. Individuals collected were fixed in 10% formaldehyde, later preserved in 70% ethanol, identified and deposited in the Ichthyological collection of Museu Paraense Emílio Goeldi (MPEG), Belém, Pará, under serial number MPEG 8575; 8576; 8577; 8579; 8586; 8634; 8635; 8637; 8678; 8687; 8702; 8705; 8708; 8722; 8724; 8725; 8737; 8755; 8760; 8764; 8769; 8804; 8846; 8853; 8868; 8872; 8874; 8888; 8891; 8909; 8911; 8943; 8972; 9365.

Feeding analyzes. The stomachs were removed and the contents of each stomach were examined in the laboratory of Ichthyology of MPEG, using Petri dishes, a precision scale and a stereoscope to identify each food item. The identification of food items was performed at the lowest possible level using specific literature and specialist assistance. The items had their frequency of occurrence (FO%; Hyslop, 1980) and mass percentage (M%; Hynes,

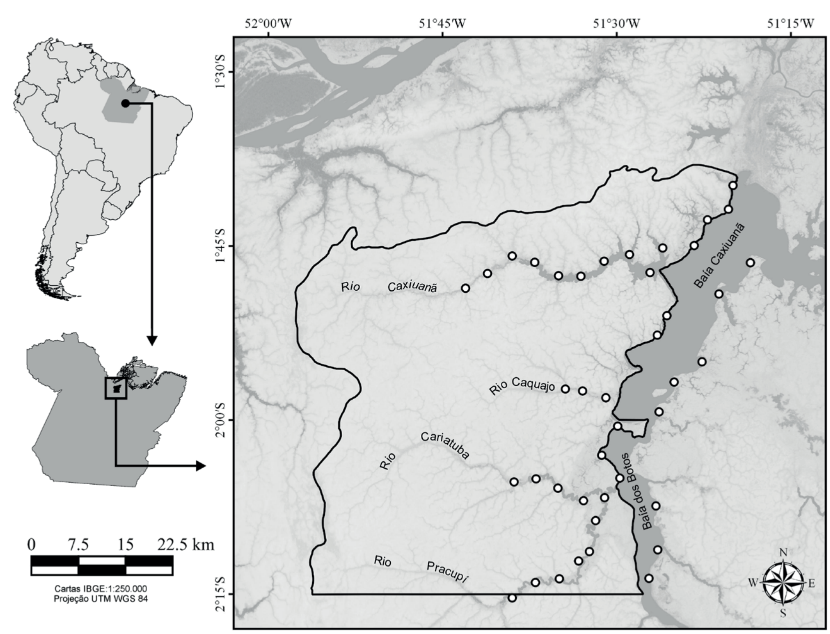

Fig. 1. Location of the Caxiuanã National Forest, municipalities of Melgaço and Portel, State of Pará, showing the ichthyofauna sampling sites.

1950) calculated. These two parameters (FO% and M%) were combined into the Alimentary Index (Ai%; modified from KAWAKAMI & VAZZOLER, 1980), which finally attributes the importance of the items in the diet. Empty stomachs were not quantified. The Ai% was calculated by the equation Ai% = (FO%*M%/∑FO%*M%)*100 and the empty stomachs were not included in the analysis. This method attempts to characterize the dominance of a particular food item in the examined stomachs from a quantitative scale that estimates the relative mass of each item.

Ecomorphological analyzes. Eighteen morphometric measurements from ten adult specimens of each species were taken (Tab. I), using a digital caliper for measurements and parchment paper for surface area. For the last, Scion Image 4.0.2 software was used to obtain values of body area (BA), pectoral fin area (PFA) and caudal fin area (CFA).

The morphometric measurements were used to obtain fifteen ecomorphological attributes, interpreted as indicators of the types of lifestyle or as adaptations to different habitats and were associated with the swimming ability, type of environment and trophic plasticity: 1) relative length of the caudal peduncle (RLCP=CPL/SL): indicates that longer peduncle, better swimmer it will be, including the benthic species living in environments with high hydrodynamics (WATSON & BALON, 1984); 2) compression index of the caudal peduncle (CICP = CPA/CPL): compressed peduncles indicates fishes with slow swimming, low maneuverability and low capacity for rapid bursts as the bodies height increases between different species (GATZ JR., 1979); 3) relative area of the pectoral fin (RAPF=PFA/BA): higher values may indicate slow swimmers, that use their pectoral fins for braking or performing maneuvers, or fish that live in running water and use their fins to deflect the flow, therefore stabilizing their position in the substrate (ALEXANDER, 1974); 4) relative area of the caudal fin (RACF=CFA/BA): larger caudal fins indicate rapid bursts (BALON *et al*., 1986); 5) aspect ratio of the pectoral fin (ARPF=PFL/PFW): higher values indicate long and narrow fins, present in species that swim over long distances (KEAST & WEBB, 1966); 6) aspect ratio of the caudal fin (ARCF=((CFW)^2/CFA): higher values indicate fishes with continuous and active swimming (GATZ JR., 1979); 7) relative position of the eyes (RPE=EH/HH): benthic fishes have eyes dorsally located, while nektonic species have lateral eyes (GATZ JR., 1979); 8) compression index (CI=BH/BW): higher values may indicate laterally compressed fishes that inhabit lentic environment (WATSON & BALON, 1984); 9) relative height (RH=BH/SL): an attribute related to the ability to develop vertical movement, being inversely related to highly hydrodynamic (lotic) environments (GATZ JR., 1979); 10) ventral flattening index (VFI=ABH/BH): lower values indicate species associated to rapids, permitting the fish to maintain their position without swimming (MAHON, 1984); 11) relative head length (RHL=HL/SL): higher values suggest predator species of relatively large prey (WATSON & BALON, 1984); 12) relative mouth width (RMW=MW/SL); higher values also suggest predator species of relatively large prey (GATZ JR., 1979); 13) relative area of mouth (RAM=MW*MH/BA): higher values indicate larger food items in the fish diet (A. C. Beaumord, unpubl. data); 14) relative height of mouth (RHM=HM/SL): attribute related to the size of the food resource, and also to the hydrodynamic morphology (WATSON & BALON, 1984); 15) mouth aspect ratio (MAR=MH/MW): attribute related to the shape of the food resource which higher values indicate fishes with narrow mouth, but large aperture, suggesting piscivorous habit (A. C. Beaumord, unpubl. data).

Variation on ecomorphological attributes between species was analyzed through a principal component analysis (PCA), which relevant axes were identified by the broken-stick model (JACKSON, 1993). The loadings higher than 0.8 were used for explanations.

Tab. I. Eighteen biometric measurements measured for the ten adult specimens of *Auchenipterichthys longimanus* (Günther, 1864), *Auchenipterus nuchalis* (Spix & Agassiz, 1829), *Tatia intermedia* (Steindachner, 1877) and *Trachelyopterus galeatus* (Linnaeus, 1766).

Measurements	Acronyms	Descriptions
Standard Length	SL	Distance from tip of snout to end of caudal peduncle
Body Height	BH	Largest dorso-ventral distance perpendicular to largest body axis
Body Width	BW	Largest body width
Average Body Height	ABH	Distance from vent to line that cuts body from mouth to tail
Caudal Peduncle Length	CPL	Distance from end of anal fin to beginning of caudal fin
Caudal Peduncle Widthw	CPW	Width of peduncle at its mid-point
Caudal Peduncle Height	CPH	Height of peduncle at its mid-point
Head Length	HL	Distance from tip of snout to end of operculum
Head Height	HH	Distance from ventral part and dorsal part of head in the region of the eyes
Eye Height	EH	Distance from center of eye to lower jaw
Mouth Width	MW	Distance between lateral parts of totally open mouth without distention of muscles
Mouth Height	MH	Distance between lips of open mouth without distention of muscles
Pectoral Fin Length	PFL	Distance between the base of the fin and its extremity
Pectoral Fin Width	PFW	Largest width of fin on axis perpendicular to the axis of the length of the fin when totally open
Caudal Fin Width	CFW	Distance between the two extremities of the fin when totally distended
Body Area	BA	Area of body plus caudal fin
Pectoral Fin Area	PFA	Area of pectoral fin when totally distended
Caudal Fin Area	CFA	Area of caudal fin when totally distended

RESULTS

Distribution. A total of 621 specimens were captured, 395 A. longimanus (mean SL 11.5 cm ± 1.8 cm), 145 T. intermedia (7.1 cm ± 0.8 cm), 53 A. nuchalis (10.4 cm ± 0.6 cm) and 28 T. galeatus (12.5 cm ± 1.8 cm). The species A. longimanus was restricted to rivers; specimens of T. intermedia were preferentially caught in the bays, but two individuals were caught in rivers. A. nuchalis and T. galeatus were captured exclusively in the bays.

Feeding. We analyzed a total of 410 stomachs, 224 from *A. longimanus*, 127 from *T. Intermedia*, 38 from *A. nuchalis* and 21 from *T. galeatus*. The Alimentary index (Ai%) values are presented in Table II. The diet of *A. longimanus* showed the greatest diversity of food items, 21 items in total. The most important items were allochthonous insects (Ai% = 52.94) and seeds (Ai% = 45.64).

Three items composed the diet of *A. nuchalis*, but terrestrial insects represented 99.89%. Nine food items were found in stomachs of *T. intermedia* of which the allochtonous insects were the most important (Ai% = 99.79). The species *T. galeatus* had a total of eight food items, and also showed terrestrial insects as the most important (Ai% = 69.64%), followed by aquatic crustacean (Ai% = 11.65).

Ecomorphology. The first two axis of the PCA had broken-stick eigenvalues significantly larger than random, and explained 61.2% of the variance in the ecomorphological data (Fig. 2). Axis 1 accounted 37.4% of the variation and axis 2 computed 23.8%. The first axis segregated species that were influenced by relative mouth width (RMW; eigenvector = 0.96) and relative head length (RHL; eigenvectors = 0.84).

The second axis also revealed intraspecific variation within species, and it was influenced by a positive correlation of aspect ratio of the pectoral fin (ARPF; 0.81) and by a negative correlation of relative height of mouth (RHM; -0.82). The result of the principal component analysis, applied to the matrix of 15 ecomorphological attributes is shown in Table III.

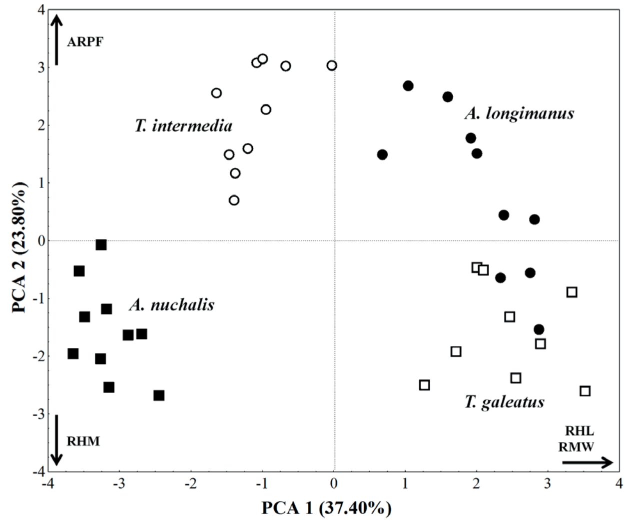

Fig. 2. Ordination diagram of the first two PCA axes for the 15 ecomorphological attributes of four auchenipterid species: (●) *Auchenipterichthys longimanus* (Günther, 1864), (■) *Auchenipterus nuchalis* (Spix & Agassiz, 1829), (○) *Tatia intermedia* (Steindachner, 1877) and (□) *Trachelyopterus galeatus* (Linnaeus, 1766). The attributes that most influenced this distribution are shown: RMW, relative mouth width; RHL, relative head length; ARPF, aspect ratio of the pectoral fin; RHM, relative height of mouth.

DISCUSSION

Understanding how ecomorphological traits showed by species in relation to environmental gradients is a basic premise for prediction of species distributions through a macroecology observation (Severo-Neto *et al.*, 2015). In the present study, we described the distribution, diet and ecomorphology for four species from Auchenipteridae in the lower Anapú River (Eastern Amazonia). The taxonomic

Tab. II. Alimentary index (Ai%) of food items consumed by the four Auchenipteridae species from the Caxiuanã National Forest, Pará, Brazil.

Food items	*A. longimanus*	*A. nuchalis*	*T. intermedia*	*T. galeatus*
Algae	<0.01			
Annelida (Oligochaeta)	<0.01		<0.01	
Araneae	<0.01		<0.01	
Chilopoda	<0.01			
Crustacea (allochthonous)	<0.01		<0.01	<0.01
Crustacea (autochthonous)	<0.01			11.65
Detritus	<0.01			
Diplopoda	<0.01		<0.01	8.18
Insecta (allochthonous)	52.94	99.89	99.79	69.64
Insecta (autochthonous larvae)	<0.01	0.00	<0.01	
Mammalia (fur)	<0.01			
Nematoda	<0.01			
Opiliones	<0.01		<0.01	
Osteichthyes	<0.01			<0.01
Osteichthyes (scales)	<0.01			2.85
Plantae (branch/root)	0.91		<0.01	1.06
Plantae (seeds)	45.65			5.87
Platyhelminthes (Tubellaria)	<0.01		<0.01	
Scorpiones	<0.01			
Squamata (Snake skin)	<0.01			
Vertebrate Fragments	<0.01	0.00		

Tab III. Mean (M) and standard deviation (SD) values for the 15 ecomorphological attributes calculated for four Auchenipteridae species from the Caxiuanã National Forest, Pará, Brazil. CI, compression index; RH, relative height; RLCP, relative length of the caudal peduncle; CICD, compression index of the caudal peduncle; VFI, ventral flattening index; RAPF, relative area of the Pectoral Fin, ARPF, Aspect Ratio of the Pectoral Fin; RACF, relative area of the caudal fin; ARCF, aspect ratio of the caudal fin, RPE, relative position of the eyes; RHL, relative head length; RMW, relative mouth width; RHM, relative height of mouth; MAR, mouth aspect ratio; RAM, relative area of mouth.

Ecomorphological atributes	*A. longimanus*		*T. intermedia*		*A. nuchalis*		*T. galeatus*		PCA Axis	
	M	SD	M	SD	M	SD	M	SD	1	2
CI	1.261	0.14	1.3	0.11	2.446	0.38	1.285	0.09	-0.748	-0.462
RH	0.287	0.05	0.207	0.01	0.197	0.01	0.284	0.03	0.788	-0.116
RLCP	0.097	0.02	0.158	0.03	0.12	0.02	0.075	0.01	-0.557	0.479
CICD	3.512	1.26	2.724	0.36	2.549	0.35	3.713	0.47	0.643	-0.147
VFI	0.628	0.07	0.569	0.05	0.619	0.08	0.487	0.11	-0.304	0.192
RAPF	0.047	0.01	0.012	0.01	0.023	0	0.046	0.01	0.712	-0.262
ARPF	5.254	2.1	5.681	1.76	3.232	0.8	2.915	0.83	-0.018	0.811
RACF	0.128	0.03	0.189	0.03	0.12	0.02	0.123	0.02	-0.147	0.707
ARCF	1.721	0.7	1.522	0.39	2.166	0.37	1.525	0.4	-0.321	-0.518
RPE	0.398	0.11	0.517	0.1	0.683	0.09	0.511	0.14	-0.673	-0.332
RHL	0.261	0.03	0.216	0.02	0.203	0.01	0.27	0.03	0.844	-0.216
RMW	0.131	0.01	1.06	0.01	0.059	0.01	0.131	0.01	0.961	0.127
RHM	0.037	0.01	0.04	0.01	0.053	0.01	0.056	0.01	-0.062	-0.823
MAR	0.283	0.05	0.404	0.08	0.899	0.09	0.431	0.07	-0.773	-0.56
RAM	0.018	0.01	0.195	0	0.016	0	0.029	0.01	0.541	-0.635
Eigenvalue									5.61	3.58
% of Variance									37.40	23.83
Broken-stick Eingenvalue									3.32	2.32

proximity between these species is an important question and could generate more competition, since members of Auchenipteridae inhabit very similar niches (Ferraris Jr., 2003): nocturnal species, hiding during the day in rock crevices and submerged branches and trees, which probably involved several similar adaptations in morphology and behavior.

Montag *et al*. (2013) observed that *A. longimanus* and *T. intermedia* shown great abundance in the aquatic systems of Caxiaunã National Forest (Eastern Amazon, Brazil), but *A. longimanus* is unique to rivers and *T. intermedia* inhabits preferably in the bays. This segregated distribution may have played an important role in their local existence, and caused a reduction in the pressure of interspecific competition for food and territory, since they are ecomorphologically similar, inhabit marginal areas and feed on allochtonous items. Hugueny & Pouilly (1999) suggested that the availability of food may be one of the factors that prevent the establishment of relationships between diet and morphology when the study is restricted to species belonging to the same trophic category.

Regarding the trophic ecology of auchenipterids, the feeding habits of the four analyzed species are similar to those found for the same genera, such as insectivorous/frugivorous for *Auchenipterichthys* (Freitas *et al*., 2011), and insectivorous for *Auchenipterus* (Mérona *et al*., 2008), *Tatia* (Ramírez *et al*., 2015) and *Trachelyopterus* (Ximenes *et al*., 2011).

According to the ecomorphological hypothesis proposed, the attributes may reflect important aspects of their ecology, such as habit and adaptation to different resources (Balon *et al*., 1986). Thus, based on the principal component analysis, and evidenced by the higher values of the attributes RMW and RHL, we found that *A. longimanus* and *T. galeatus* tend to feed on larger items, such as seeds and aquatic crustaceans, respectively.

Higher values of ARPF for *A. longimanus* and *T. intermedia* may reveal the longer swimming capacity between the other analyzed species. Despite this attribute was originally related to migrations (Keast & Webb, 1966), this swimming activity may vary in amplitude, which can be defined as the extent of the displacement and/or the regularity of which it occurs among fish species. There are migrants that travel long distances and others that travel only a few meters. There are those that move laterally, limiting their migration to stretches of small tributaries for breeding and/or feeding purposes (Capeleti & Petrere Jr., 2006). Here we consider that these two species have larger displacement capacity during their periods of activity.

On the other hand, lower values of ARPF for *A. nuchalis* and *T. galeatus* attribute a low capacity of performing extended moving, and could assume that these species inhabit more structured environments. Breda *et al*. (2005) confirms this environmental preference at least for *T. galeatus*, indicating that the morphology of the caudal fin of this species allow it to perform upward and downward movements of the posterior part of the body, providing improved performance in environments of high complexity.

Despite the close phylogenetic relationship between the analyzes species, and based on distribution, feeding habits and ecomorphological traits, we observed a smooth dissimilarity within *A. nuchalis*, *A. longimanus*, *T. intermedia* and *T. galeatus* in the lower Anapú River. However, the set of characteristics presented in this study highlighted some important information about how ecomorphological similar species behave and share resources. We believe that morphological adaptations and trophic diversity play a significant role on the coexistence of species in the Amazonian fish assemblages.

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