

Environmental influences on the distribution of arapaima in Amazon floodplains

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Abstract This study investigated the environmental factors influencing the distribution of the endangered arapaima (*Arapaima* spp.) in floodplains of the Amazon. The abundance of arapaima was found to be positively related to the area and depth of the water column, and hence volume of lakes. Greater depth of water column also was related positively with the abundance and presence of arapaima in connecting channels. The abundance of arapaima was positively related to the connectivity of the lake with other water bodies. The principal reason for arapaima to prefer habitats that are deep, large, and connected to other water bodies appears to be increased survival through lower susceptibility to extreme drought events and

increased mobility and availability of food resources. Deeper, larger, and more connected lakes and connecting channels sustain greater arapaima populations; they can now be used to prioritize conservation efforts.

Keywords Brazil · Conservation · Osteoglossidae · Abundance · Connectivity · Depth

Introduction

Understanding the influence of environmental factors on the distribution of fish populations is increasingly

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important as anthropogenic pressures on fish resources continue to increase, often to the point of overexploitation and even extinction. Improved knowledge on the subject can improve the effectiveness of conservation schemes, such as through identification of critical habitat (Kouamé et al. 2008).

Various studies worldwide have shown that environmental factors related to the size of the habitat, such as depth and area, are variously related to fish abundance and species richness (Gorman and Karr 1978; Tonn and Magnuson 1982). Other environmental factors related to the biophysical structure of the aquatic habitats, such as macrophyte vegetation, leaves and organic debris, also have been shown to influence fish distribution patterns, as they offer protection from predators, foraging and spawning site availability, etc. (Chapman 1988; Savino and Stein 1989; Benson and Magnuson 1992). Physico-chemical factors related to water quality also have been shown to variously influence fish distribution (Tonn and Magnuson 1982; Rahel 1986; Brazner and Beals 1997).

There have been few studies on the environmental factors influencing fish distribution in tropical floodplains (Lowe-McConnell 1987; Goulding et al. 1988). The principal and best-understood environmental factor in floodplains is the flood pulse, which has strong seasonal effects on the distribution of fish species (Junk et al. 1989). Low water levels restrict water availability, and hence fish distribution, to a few habitats, and high water levels greatly expand the flooded area and habitat availability to fish populations (Saint-Paul et al. 2000; Silvano et al. 2000; Galacatos et al. 2004). Fish adapt to these drastic environmental changes through ‘lateral migrations’ among floodplain habitats (Fernandez 1997). Other bio-physico-chemical factors known to influence fish distribution in floodplains include water transparency, which was shown to be a remarkable predictor of the abundance of piscivorous fish in floodplains of the Orinoco basin (Rodríguez and Lewis 1997; Tejerina-Garro et al. 1998). Water depth and nutrient concentration in floodplain lakes of the Paraná River have been found to influence abundance of several fish species (Petry et al. 2003a). Water body connectivity and depth also have been shown to influence the abundance of several fish species in floodplain lakes of the Pantanal region (Súarez et al. 2001, 2004). Finally, dissolved oxygen, transparency, depth, and

macrophyte cover have been shown to influence the abundance of fish species in floodplains of the Amazon River (Petry et al. 2003a, b).

Despite those observations, however, most studies on the influence of environmental factors on the distributions of fishes in floodplains have focused on fish assemblages and communities. Only a few studies such as Petry et al. (2003b) and Rodríguez and Lewis (1997) have provided trophic group-specific information. Fish communities in tropical floodplains have many species that are rare, some species that are moderately abundant, and few species that are highly abundant and comprise most of fisheries catch (Bayley and Petrere 1989; Winemiller 1996). Many of these fished species are becoming overexploited, and developing conservation strategies requires, among other things, species-specific understanding of their distributions in the floodplains.

Here, we study the influence of environmental factors on the distribution of arapaima (*Arapaima* spp.¹) in floodplains of the Amazon. The arapaima migrate through eight habitats in the course of the annual flooding cycle, maintaining annual water current velocity at about 0.12 m/s and depth at about 3 m (Castello 2008a, b). They inhabit mostly lakes and connecting channels during low water levels. At that time, the adults form pairs, and during rising water levels they build their nest in the margins and banks of lakes, temporary lakes, and connecting channels. When the larvae hatch, the males protect and guide the young by swimming slowly through the food-rich environments of flooded forest for about 3 months. When water levels lower, the adult arapaima and their young all migrate back to lakes and communicating channels, where they become vulnerable to fishing activity because of the dramatic contraction in flooded area (Castello 2008a). Exacerbating this vulnerability are their large sizes of up to 3 m in length and 200 kg in weight (Arantes et al. 2010), and their obligate air-breathing behavior that exposes them to harpoon-specialist fishermen every 5–15 min when they surface to gulp air (Sánchez 1969). Recognizing the vulnerability of arapaima in lakes, many Amazonian fishers have implemented conservation-related restrictions banning fishing in selected lakes (McGrath et al. 1993). Protection of

¹ Taxonomic status of the studied population remains uncertain (Castello and Stewart 2010), so we use only the genus name.

selected lakes is a very common approach to safeguard arapaima populations (Chapman 1988; Castello 2008b). Nevertheless, no study to date has evaluated the rationale for this approach, or the criteria for selection of lakes for protection. In this study, we evaluate if and which environmental factors influence the distribution of arapaima within Amazonian floodplains.

Methods

This study investigated the environmental factors influencing the distribution of arapaima during low water levels in floodplains of the Amazon. The study focused on the two main habitats used by arapaima during low water levels: lakes and connecting channels (Castello 2008a). Several analytical methodologies were used to investigate relations, if any, among the abundances of arapaima and a total of 14 environmental factors in lakes and connecting channels. Field data were collected between 20 October and 27 December, 2007.

Study area

The study was done in an area of 562 km², called Jarauá, within the Mamirauá Sustainable Development Reserve, which is located in the Solimões River in the Amazon Basin, near the city of Tefé (approx. 3°S–66°W; Fig. 1). The study area is formed completely by várzea, which are whitewater-influenced floodplains formed by a mosaic of forests, lakes, and streams that are continually re-worked by dynamic processes of erosion and sedimentation (Junk 1997). The várzea are characteristically highly heterogeneous and diverse with respect to habitat arrangement and composition; eight different habitats are recognized in the region (based on Castello 2008a; Table 1). The flooding pulse is monomodal and varies by about 12 m annually, creating marked differences between high water levels when all habitats are flooded, and low water levels when only a few habitats remain flooded (i.e., lakes and connecting channels).

Study approach, data sources, and field collection

Two main methodological approaches were used, reflecting the distinct characteristics of lakes and

connecting channels. Lakes tend to be disconnected from other water bodies during low water levels, and that allows us to relate lake-specific data on environmental factors to lake-specific estimates of arapaima abundance. As such, a total of 32 lakes were chosen, based on the feasibility of access for sampling. Connecting channels can be very long (over tens of km), usually remain connected to other water bodies (such as main river channels or some lakes), and arapaima in them are heterogeneously distributed. To assess possible relations among environmental factors and arapaima abundances, 20 1-km long sections of the only connecting channel in the study area were chosen. In these sections arapaima abundances were considered only in terms of the presence ($n=10$) and absence ($n=10$) of individuals (Fig. 1).

Data on the abundance and presence-absence of arapaima were collected using a method to census arapaima populations based on counts of the individuals at the moment of aerial breathing (Castello 2004). Such counts of arapaima include only individuals longer than 1 m in total length, and have been estimated to vary by about 10–30% around the real value (Castello 2004; Arantes et al. 2007). The data are expected to be relatively reliable given that the counts were made by expert fishermen who have had the accuracy of their counts of arapaima assessed by comparison to independent estimates of abundance for the same populations (Arantes et al. 2007; Castello et al. 2011). Using this method, local fishermen censused the arapaima population at each chosen lake and section of the connecting channel, covering the entire surface area of these habitats, with the difference that the data were considered only in terms of presence-absence in the chosen sections of the connecting channel. The sections of the connecting channel sampled can be considered to be independent from each other, because the counts were made during a short time frame (i.e., same day) that minimized potential movements of arapaima among sampled sections. The data on abundance and presence-absence of arapaima likely were not affected by the local fishing activity, because the counts were done immediately after the flood season when fishing for arapaima had not yet been done and arapaima had just migrated out of the flooded forests into lakes and connecting channels. The observed data on abundance and presence-absence, thus, are the result of a recent

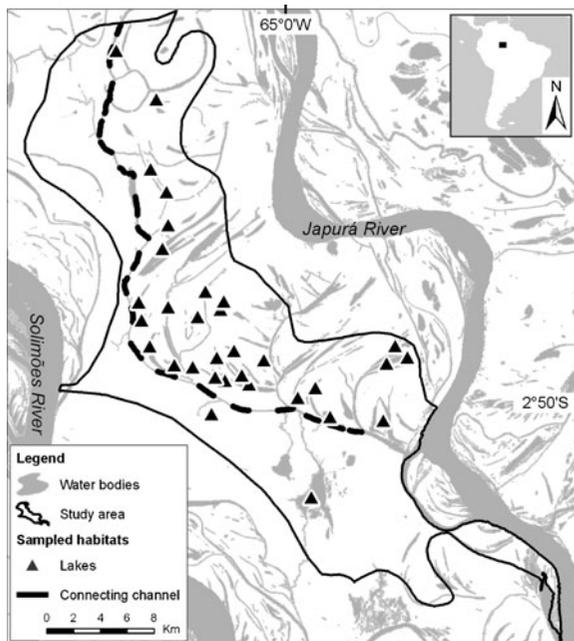


Fig. 1 The study area and the locations of the sampled habitats (lakes and connecting channels). Aquatic habitats are in grey. The larger channels are the Solimões and Japurá Rivers. The other aquatic habitats are the connecting-channel (sample sites marked with *heavy dashes*), lake-channels, temporary lakes, and persistent lakes (sample sites are marked with *triangles*). Terrestrial habitats (*white*) between these channels and water bodies are composed of shrub forests, low levee forests, and high levee forests. The study area (*encircled by solid line*) comprises about 562 km². Inset shows location of the study area in South America

redistribution of the species within the ecosystem after the flood.

Sampling of environmental factors in lakes and sections of connecting channels was done immediately after counting, and it was done from canoes in the middle, and by foot on the margins, of the water bodies. Sampling of environmental factors was done as uniformly as possible over the surface of the water and along the margins of the water bodies, so as to obtain representative samples for each studied location. A total of 14 environmental variables were sampled as described in Table 2 where measurement details are given. These variables were chosen based on previous studies (reviewed earlier), feasibility of sampling, and educated guesses by the authors about which variables could potentially influence arapaima abundance. Forest types and substrate can influence resource availability such as space for nest building or food supply for prey species (Scott et

al. 2005; Castello 2008b). Floating macrophyte offer nursery habitat for the young, food supply for several (generally small) fishes, and both floating macrophytes and (dead) tree branches (which typically are along the banks) offer protection against predators (Crampton 1999). Water quality variables, which variously influence, and can be related to, fish abundance and assemblages included temperature, transparency, current velocity, dissolved oxygen, pH, and conductivity (Junk et al. 1983; Rodríguez and Lewis 1997). However, because of the nature of lakes and connecting channels, the sampling of environmental factors in both habitats was not identical, as noted in Table 2, with more factors being sampled in lakes than in connecting channels.

Habitat availability is mainly determined by the volume of water, which is determined by habitat area and the height of the column of water (i.e., from surface to the bottom). “Depth of the water column” was measured in the field. However, water levels in a lake during dry season are not necessarily the same as in connecting channels and the main river channel. This is because lakes tend to be disconnected from other water bodies during dry season, so that they may hold water even though water levels may continue to lower elsewhere. Thus, habitat connectivity in dry season is mainly determined by the depth of the aquatic habitat relative to the entire ecosystem. This was measured as “depth of flooding”, which we defined as the depth measured from the bottom of the aquatic habitat to the maximum level reached by the last flood. Measuring the maximum level of the last flood in the várzea is easy through conspicuous (ring-like) marks on the trees. Data on depth of flooding enable all depth measurements to be compared, thus allowing to assess the likelihood that the habitat will remain flooded at any point in time. As such, we measured depth of flooding of the lakes and of the lake-channels, given that the latter play a critical role in determining whether during low water levels a lake remains connected to surrounding habitats.

Data analyses

Preliminary data analyses together with the varied nature of the data collected led us to multiple

Table 1 The eight principal habitats of the várzea floodplains in the study area

Habitat	Description
River	The main river channels. The river is wide (up to 3 km), deep (up to 50 m) and swift flowing (Sioli 1984).
Connecting channel	Channels transporting river waters and crossing sections of várzea. Both ends connect to the river (Sioli 1984).
Lake	Lakes of various sizes and shapes (Sioli 1984). Lakes normally hold water throughout the flood cycle.
Lake-channel	Channels connecting lakes to any other water body including another lake; they dry up making the lakes physically isolated (Crampton 1998).
Temporary lake	A shallow type of lake with a large and open mouth. Most dry up during the dry season (Local classification).
Shrub	Low swampy woodland, usually located behind levees (Ayres 1995).
Low levee	Silt-heightened riverbanks and bars on which tall forest grows (Ayres 1995).
High levee	Like low levees, but riverbanks and bars are higher and the forests are taller, older, and more diverse (Ayres 1995).

approaches to data analysis. Lakes were split into two 16-lake groups: high and low abundance, measured in terms of total number of individuals, not density (Table 3). The difference in abundance found between these two groups was of over one order of magnitude (*t*-test, $p < 0.05$). This allowed to compare environmental factors in lakes with extreme abundances of arapaima and to do inferential analyses that, unlike multivariate analyses, provide probability values (i.e., *p*-value) associated with the error of rejecting null hypotheses. As such, lake-related data were analyzed using four approaches. Approach one: we used a two-factor ANOVA test to assess if qualitative factors (i.e., forest types, substrate types, and floating macrophytes) cover explained whether a lake was of high or low arapaima abundance. Approach two: we used a *t*-test to assess if there were differences between the quantitative water-related factors in high and low abundance lakes (Table 2). Approach three: we also used a *t*-test to assess if mean depth of flooding of lakes and respective lake-channels and length of the lake-channels explained whether a lake was of high or low arapaima abundance. Finally, we used a multiple linear regression model to assess if arapaima abundance values, not the lake groups, were related to lake area, depth, and number of tree branches. Shapiro-Wilk (*W*) tests were used to assess the normality of residuals from multiple linear regression model and ANOVA analyses. Abundances data were Ln (\bar{x}) transformed for normalization.

Connecting channel-related data were analyzed using two approaches. Approach one: we used a Chi-square test to assess if qualitative factors of forest type and tree branches were different between transects with absence and presence of arapaima. Approach two: we

used a *t*-test to assess if sections with absence and presence of arapaima differed with respect to quantitative factors of transparency, dissolved oxygen, temperature, conductivity, pH, current velocity, and depth.

Results

We found that, out of the 14 environmental factors investigated, eight were variously related to the abundance of arapaima.

Lake analyses

No relation was found between arapaima abundance in lakes and forest types, substrate type, or floating macrophytes coverage (Table 4). The assumptions of the ANOVA test were met, and the residuals of the various analyses were normally distributed (forest type, $W=0.968$, $p=0.47$; substrate type, $W=0.968$, $p=0.451$; floating macrophytes, $W=0.966$, $p=0.407$). The sampled lakes were characterized as follows. Most lakes were dominated by shrub (43%) or low levee (40%) forests, and the rest (17%) by high levee forests. The substrate of most lakes was composed by organic debris (47%) and clay (40%). The area covered by floating macrophytes was relatively low, between 0 and 25% in 66% of the lakes.

Of the quantitative physical and chemical factors related to water quality, only conductivity ($p < 0.05$) was found to be higher in lakes with high arapaima abundance (Table 5). Measured values of water transparency, dissolved oxygen, and conductivity all varied greatly, while temperature and pH values varied little (Table 5). In general, water transparency

Table 2 Environmental factors measured together with description of measurement procedures. The environmental factors sampled in the lakes and connecting channels are indicated. The environmental factors measured were grouped in

(i) qualitative, (ii) quantitative related to water (including physical and chemical factors), and (iii) quantitative related to lake structure (including tree branches and factors related to connectivity)

Factor	Measurement procedure	Lake	Connecting channel
Qualitative			
Forest types: shrub, low levee, or high levee	Classification based on overall predominance	X	X
Substrate type: sand, clay, or organic debris	Classification based on three samples taken in center of lake	X	
Floating macrophytes cover	Classified based on categories of 0–25, 26–50, 51–75, and over 75% through visual inspection	X	
Cover by tree branches	Classified in smaller or greater than 50% of the section area		X
Quantitative: water related			
Transparency (cm), Dissolved oxygen (mg/l), Conductivity (μS/cm), Temperature (°C), pH, Current velocity (m/s)	Except for transparency which was measured only the surface, these were measured at surface and bottom of water column, in various locations, roughly every 100 m on a straight line in the middle of the habitat. Current velocity was measured only in connecting channels (it is zero in lakes)	X	X
Quantitative: lake structure related			
Tree branches	Counts done from a canoe of visible tree branches	X	
Depth of water column (m)	Measured in various locations, roughly every 100 m on a straight line in the middle of the habitat	X	X
Depth of flooding (m)	Measured in a minimum of three locations; because most trees with marks of maximum flood were on shrub or levee forests, measuring depth of flood of a lake required measuring depth of the water column and then measuring the height of the maximum flood mark on the trees. Depth of flooding also was measured in the lake-channels of every sampled lake	X	
Surface area (ha), Length of lake-channels (km)	Estimated based on satellite imagery analysis (i.e. landsat). Length of lake-channels correspond to the distance from the lake to the next water body following the curvature of the channel	X	

was low (~53 cm), pH was neutral, and dissolved oxygen concentrations were very low, nearly anoxic. Values of conductivity and temperature were roughly similar to previous studies in similar floodplain lakes (e.g. Henderson 1999).

Lakes with high arapaima abundance had greater depths of flooding than lakes with low arapaima abundance. The lake-channels of lakes of high arapaima abundance were shorter and also had greater depth of flooding than those of lakes with low arapaima abundance (Table 5). The average differences in depth of flooding were about 2 m, and differences in length of lake-channels were about 1 km.

Lakes with greater depth and area, and hence volume, were positively related to abundance of arapaima, as indicated by the good fit of the multiple linear regression model (Table 6). The residuals were normally distributed ($W=0.977$, $p=0.711$), and the model explained 58% of the variance in abundance. Numbers of tree branches in the lakes were not related to arapaima abundance (Table 6).

Connecting channel analyses

Of the factors measured in sections of the connecting channel, area covered by tree branches was positively

Table 3 Studied lakes split in two 16-lake groups. Mean difference in number of arapaima was statistically significant (T-Test, $p < 0.05$). *Lakes contributing to 74% of all arapaima

Low abundance		High abundance	
Lake name	# ind.	Lake name	# ind.
Cobras	5	Buá-Buá*	1,207
Calça I	17	Cedrinho do Jaraqui	195
Curuça do Barreirinho	29	Comprido do Maciel	320
Curuça do Centro	30	Jurupari	266
Guariba I	12	Maneco	79
Guariba II	32	Panelão*	615
Guariba III	31	Panelinha I	70
Jacitarinha	17	Panelinha II	71
Paracuuba	5	Poço do Jaraqui	120
Rato	31	Poço do Maciel	115
Redondo do Maciel	8	Poço do Matá-Matá	197
Taracuzinho	4	Samauma*	2,256
Tracajá	35	Samaumeirinha Jaraqui*	113
Tucunarezinho	7	Samaumeirinha Tucuxi*	1,233
Urucurana I	13	Sarapião	196
Urucurana II	24	Tucunarezinho Samaúma	121
Arithmetic mean	19	Arithmetic Mean	448
Geometric mean	15	Geometric Mean	237

related to arapaima presence ($\chi^2=7,200, p=0.0007$) and depth was found to be positively related to the presence of arapaima, with a difference of about 2.5 m between groups of sections with and without arapaima (Table 7). Not one of the other quantitative factors measured (i.e., transparency, dissolved oxygen, temperature, conductivity, pH, and current velocity) was related to the presence or absence of arapaima. Values of transparency, temperature, conductivity, and pH varied little, and values of current velocity and dissolved oxygen varied more, although both remained very low (Table 7). Type of surrounding forest was not related to arapaima presence ($\chi^2=2,067, p=0.350$).

Discussion

Factors related to arapaima abundance

The distribution of arapaima in the varzea during low water levels appears to be influenced primarily by the depth and area of lakes (i.e., their dry-season volume;

Table 6), the connectivity of such lakes to other water bodies (Table 5), and by depth of water column in sections of connecting channels (Table 7). There are advantages for the arapaima to inhabit places with more availability of, and connectivity among, aquatic habitats. A major advantage can be increasing survival. Low water levels are generally associated with mortality of floodplain fish populations, because water quality becomes very poor, especially during extreme drought events, such as El Niño years in the Amazon basin (Welcomme 1979; Furch and Junk 1997; Schongart and Junk 2007). Even though the arapaima can withstand anoxia, they may suffer from other aspects of poor water quality, such as hydrogen sulfide, that generally are negatively associated with volume of water (Furch and Junk 1993). Deeper and larger lakes also may be better feeding grounds (Table 6) that offer greater total prey fish biomass. Lake volume was positively related to fish diversity and abundance in Pantanal lagoons (Súarez et al. 2004). These deeper and larger lakes also can improve reproductive success. Deeper, larger lakes in the study

Table 4 Two-way ANOVA for qualitative factors of forest types, substrate types, and floating macrophytes cover as independent variables and arapaima abundance (high or low) in lakes as dependent variable. Abundance data were Ln (*x*) transformed

Source of variation	D.F.	S.S.	M.S.	F	<i>p</i>
Forest type	2	0.882	0.441	0.439	0.649
Low or high abundance	1	60.379	60.379	60.141	0.000
Low or high abundance × forest type	2	0.932	0.466	0.464	0.634
Residuals	26	26.103	1.004		
Substrate type	2	5.056	2.528	2.589	0.094
Low or high abundance	1	56.708	56.708	58.087	0.000
Low or high abundance × substrate type	2	1.149	0.574	0.588	0.562
Residuals	26	25.383	0.976		
Floating macrophytes cover	3	6.528	2.176	2.504	0.083
Low or high abundance	1	54.958	54.958	63.252	0.000
Low or high abundance × floating macrophytes cover	3	5.958	1.986	2.286	0.104
Residuals	24	20.853	0.869		

area tend to hold larger arapaima populations at a time when they engage in courtship and mating activities (Flores 1980; Castello 2008b). Finally, the greater connectivity of these deeper, larger lakes to other water bodies is expected to positively influence all three processes suggested above: survival, feeding, and reproduction. By better allowing the arapaima to move between and among aquatic habitats, arapaima probably can better locate food resources, find a mate or spawning habitat, or swim to drought-protected places. The effects of connectivity have been observed in another study of fish assemblages near the study area. Lakes closer to main river channels, i.e., with shorter lake-channels, possessed higher diversity of fish species (Granado-Lorencio et al. 2007).

Factors unrelated to arapaima abundance

The positive relations found between the presence of arapaima in sections of connecting channel and cover by tree branches, and higher conductivity in lakes of high abundance of arapaima (Tables 6 and 7), probably are associations with depth. Differences found in conductivity probably reflect differential effects of rainfall and evapo-transpiration processes associated with lake depth and volume (Crampton 1998). Similarly, the presence of tree branches in the water generally is due to shore-line erosion, which tends to be more prevalent in deeper aquatic habitats. However, tree branches potentially can provide protection against predators (Crampton

Table 5 Comparison between quantitative factors related habitat connectivity and water quality in lakes of high and low abundance of arapaima. *P*-values are based on pair-wise t-tests for each variable (*n*=16 in all cases)

Factor	Low abundance		High abundance		<i>p</i>
	Mean	S. D.	Mean	S. D.	
Water quality					
Transparency (cm)	57.3	33.3	50.7	26.1	0.481
Dissolved oxygen (mg/l)	0.9	1.1	1.4	1.2	0.209
Conductivity (μS/cm)	107.2	66.1	165.5	90.7	0.046
Temperature (C)	30.1	1.8	30.6	1.4	0.543
pH	7.3	0.9	7.4	0.8	0.736
Connectivity					
Depth of flooding of lakes (m)	6.0	1.1	7.9	2.4	0.008
Depth of flooding of lake-channels (m)	6.2	1.0	8.5	2.5	0.004
Length of lake-channels (km)	2.8	1.6	1.7	1.2	0.040

Table 6 Multiple linear regression model with arapaima abundance as dependent variable and area, number of tree branches, and depth of water column as independent variables. Abundance data were Ln (*x*) transformed

Source of variation	Coefficient	<i>p</i>
Constant	2.585	0.000
Number of tree branches	0.000	0.999
Area	0.010	0.000
Depth	0.007	0.006

1999), and habitat complexity created by tree parts such as roots, leaves, and stems have been positively related to fish diversity and abundance (Petry et al. 2003b).

Several environmental factors (i.e., forest and substrate type, macrophyte and tree branches cover, transparency, oxygen, temperature, and pH) were not related to arapaima abundance, perhaps because they varied little (Tables 4, 5 and 7). This was surprising especially with respect to macrophyte cover and transparency, both of which previously had been found to be related positively to abundance of piscivores (Rodríguez and Lewis 1997; Petry et al. 2003b), such as arapaima.

Implications for management and conservation

Deeper and larger lakes, and deeper sections of connecting channels, tend to have very high concentrations of arapaima. This can be shown quantitatively: 74% of all arapaima were found in only 13% of the studied lakes (i.e., 5 out of 32; Table 3). Thus, deeper, larger lakes, and deeper sections of connecting channels are priority habitats for management. These habitats must be considered in the development and

implementation of large-scale frameworks of protected areas for Amazonian freshwater fauna (Hrbek et al. 2007). Habitats with these characteristics also can be considered for monitoring arapaima populations, allowing for a cost-effective use of scarce human and financial resources. The abundance of arapaima in habitats with these characteristics also can be interpreted as an indicator of population health. For example, if such habitats are depleted of arapaima, there is probably excessive illegal harvest and need to implement conservation measures.

However, we note that our results are for arapaima greater than 1 m in total length and they are only partially valid for young of the year shorter than 1 m. There are no data on the spatial distribution of these young of the year arapaima. Our field experience indicates that such fishes prefer to inhabit shallow habitats that have few or no adult arapaima. This is something to be studied in the future given the importance of recruitment to population health.

Depth is key for floodplain fishes

That dry-season depth is a key factor influencing the distribution of arapaima, out of a total of 14 factors, should be no surprise in an aquatic ecosystem where water availability varies enormously seasonally and inter-annually. During the last 20 years in the study area, seasonal variation in water levels has been about 10 m, and inter-annual variation in minimum water levels has been about 7 m (Ramalho et al. 2009). Given that mean depths of lakes and connecting channels was only about 10 m (Tables 5 and 7), it seems obvious that arapaima and other fish species should inhabit places with the greatest protection against potential drought if

Table 7 Comparison between quantitative factors related to water quality and depth in sections of connecting channel with and without arapaima. *P*-values are based on pair-wise t-tests for each variable

Factor	Absence		Presence		<i>p</i>
	Mean	S. D.	Mean	S. D.	
Transparency (cm)	39.5	5.0	41.5	4.8	0.374
Dissolved oxygen (mg/l)	0.7	0.4	0.4	0.3	0.343
Conductivity (µS/cm)	28.5	0.7	28.6	0.7	0.298
Temperature (C)	138.6	11.4	128.2	28.1	0.755
pH	6.9	0.1	6.9	0.2	0.686
Current velocity (m/s)	0.1	0.1	0.1	0.1	0.667
Depth of water column (m)	7.9	14.7	10.6	34.3	0.000

they are to survive in this ecosystem. Thus, depth probably also is a key factor in the distribution of many other floodplain fish populations.

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