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Diversity in reproductive traits of arapaima (*Arapaima* spp., Müller, 1843) in Amazonian várzea floodplains: Conservation implications

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Abstract

1. Understanding the reproductive ecology of freshwater fishes is essential to minimize the losses in global freshwater biodiversity but is often limited in data-poor regions, such as tropical floodplain ecosystems. Specifically, the study investigated whether size at first sexual maturation and nesting features for arapaima vary within and across regions in the floodplain of the Amazon River.
2. Data were collected at several sites in the Lower Amazon with varying arapaima densities and fishing practices. Female gonads were examined from commercial catch to calculate total length of first sexual maturation (L_{50}). Nest features were surveyed in the field. The size at first maturation and nest features (i.e. nest morphology, habitat, and density) were compared among sites with different population densities in the Lower Amazon and among estimates drawn from the literature for other regions.
3. In the Lower Amazon, L_{50} showed significant variation between high-density (139 cm) and other sites (~168 cm). Overall variation in L_{50} estimates for arapaima range from 139 cm in the Lower Amazon to 207 cm in the Upper Amazon in Peru. Nests in different regions show variation among certain nest features and a positive relationship between nest density and arapaima population density. In the Lower Amazon, 90% of nests were found under woody vegetation.
4. The results show considerable diversity in size at first maturity and nesting features for arapaima. This suggests that there may be multiple evolutionarily significant units or species, even within the study area. This study also illustrates the importance of forest cover to arapaima spawning. Furthermore, different nesting morphologies were found at different sites. There are meaningful variations in arapaima reproductive behaviour, both locally and basin-wide, that require further study as they have implications for effective management and conservation initiatives.

KEYWORDS

fish, fishing, flooding cycles, lake, Osteoglossidae, reproduction, river, South America, tropics

1 | INTRODUCTION

Global freshwater biodiversity is widely threatened (Arthington, Dulvy, Gladstone, & Winfield, 2016; Dudgeon et al., 2006; He et al., 2017; Strayer & Dudgeon, 2010), requiring an improved understanding of the reproductive ecology of freshwater fishes to minimize biodiversity losses. Disruptions to natural hydrology, such as those resulting from dam construction, can change the conditions of flow, temperature, or turbidity, on which many fishes depend to reproduce (Portz & Tyus, 2004). Many freshwater fishes are vulnerable to fishing while reproducing (van Overzee & Rijnsdorp, 2015), and the degradation of spawning or nursery habitats can cause population declines (e.g. Berkman & Rabeni, 1987; Jones, Helfman, Harper, & Bolstad, 1999). Knowing the reproductive traits of fishes is therefore essential to conservation and management planning. Such knowledge can be used to establish regulations, conserve critical habitats, and monitor the status of populations. For example, seasonal closures generally coincide with reproductive seasons, giving fish populations an opportunity to be replenished. Similarly, the minimum size of capture protects juvenile fishes until they can contribute offspring to the population. In addition, monitoring changes in reproduction, such as changes in age or size at maturation, can indicate levels of exploitation or stress in a fish population (Law, 2000). Despite its potential to minimize losses of freshwater biodiversity, the current understanding of the reproductive ecology of fishes is often limited in tropical floodplain ecosystems (Castello et al., 2013; Reis, 2013).

As in other ecosystems, fish reproduction in tropical floodplains is influenced by a complexity of biotic and abiotic drivers, including environmental factors, taxonomic diversity (both within and between species), and human impacts. Environmental factors are the principal drivers of reproduction, and most fishes have evolved to reproduce under specific conditions (Jobling, 1995; Wootton, 1990). Variations in temperature, vegetation, water level, habitat, flood pulse, and fish density are only some of the variables that affect reproduction (Portz & Tyus, 2004). In many tropical floodplains, the main driver of fish reproduction is the seasonal flooding and receding of water levels, called 'flood pulses' (Junk, Bayley, & Sparks, 1989). When water levels rise, fishes migrate laterally onto the surrounding floodplains and take advantage of newly accessible resources (Castello, 2008a; Welcomme, 1979). At this time, most floodplain fishes reproduce and many build nests in the vegetated floodplain habitats (Castello, 2008a; Welcomme, 1979). Floodplain forest and other vegetated habitats provide food and shelter for juvenile fishes (Welcomme, 1979). As waters recede, fishes return to permanent water bodies where they compete for resources until the next flood (Welcomme, 1979). Although it is understood that different species can exhibit distinctive reproductive strategies, striking differences can exist within closely related groups and even within individuals of the same species inhabiting different locations. For example, freshwater tropical fishes of the genus *Cichla* (Bloch & Schneider, 1801) have shown distinct reproductive strategies among and within species (Gomiero & Braga, 2004; Vieira, Melo, Santos, & Bazzoli, 2009). Such differences can be genetic or environmental, and can affect approaches to conserving biological diversity (e.g. Bowen & Roman, 2005; Bruton, 1995; Meffe, 1990). Human activities, such

as fishing and habitat degradation, often have an adverse impact on fish reproduction. For example, fishing can lead to smaller reproductive size or younger age at maturation through biological compensation (Trippel, 1995), whereas habitat degradation (e.g. alteration and deforestation) can limit the spawning and nursery grounds needed for fish to reproduce successfully. Understanding specific reproductive traits of fishes and what variation exists is critical for establishing and evaluating conservation and management strategies.

The reproductive ecology of many floodplain fishes in South America is not known, however. As a result, promising conservation and regulatory measures could be hindered by not accounting for specific reproductive traits. This study sought to answer two questions related to the variability in reproductive traits of a floodplain fish genus: (i) does size at first maturation vary among different sites; and (ii) do nesting features vary among different sites? Specifically, nesting features and size at first maturation of South American arapaima (genus *Arapaima* Müller, 1843) were investigated. No study has examined whether the reproductive traits of arapaima vary across multiple sites. Although most regulatory measures for arapaima set the minimum size of capture at 1.5 m, one study in the Central Amazon has shown that this may be at least 7 cm lower than the estimated size at first maturation (Arantes, Castello, Stewart, Cetra, & Queiroz, 2010). It is unknown if this discrepancy between practice and ideal scenarios is consistent across the range of arapaima, and, as a result, if and how regulations should be modified.

Arapaima provides a good model for studying reproductive variability in tropical floodplain fishes for several reasons. Despite present deficits in data, arapaima are among the better-studied tropical floodplain fishes. This is because of their economic value as a fishery resource and their large size, growing to 3 m in total length and 200 kg in weight (Arantes et al., 2010). The life history of the arapaima typifies that of many floodplain fishes that spawn as rising waters encroach onto the surrounding floodplain (Castello, 2008a; Welcomme, 1979). Adult arapaima dig a pan-shaped nest using their mouth and, after spawning, provide parental care to eggs and juveniles for several weeks (Castello, 2008a, 2008b; Fontenele, 1948; Queiroz, 2000). Although there has been no evaluation of how the reproductive traits for arapaima might vary across their range, three groups of factors make it a likely possibility. First, the natural range of arapaima is huge and spans various habitats, ecological regions, and flood pulse patterns (Abell et al., 2008; Junk et al., 2014). Arapaima could therefore be expected to adapt or evolve unique reproductive traits to specific conditions. Second, there is increasing recognition of diversity within the genus. Although it was considered a monotypic genus for over a century, five species of *Arapaima* should be recognized (Stewart, 2013a, 2013b). In addition, unique genetic stocks of arapaima have been found in different regions (Araripe, do Rêgo, Queiroz, Sampaio, & Schneider, 2013; Santos, Sá Leitão, Paula-Silva, & Almeida-Val, 2014; Vitorino, Nogueira, Souza, Araripe, & Venere, 2017). In Guyana, two genotypes were found to occur in sympatry (Watson, Stewart, & Kretzer, 2016). Therefore, this genetic diversity might be correlated with differentiated reproductive traits or strategies. Third, arapaima are threatened by overfishing and habitat degradation, both of which have altered

the reproductive ecology of other fishes (Law, 2000). Arapaima are easy targets for fishers, who can track and harpoon adults when they surface to breathe air, spawn over nesting sites, or provide parental care for easily visible schools of young (Video S1). Habitat degradation of floodplain forests and vegetation (see Renó, Novo, Suemitsu, Rennó, & Silva, 2011) further threatens the spawning and nursery grounds of arapaima. Arapaima spawn in floodplain forest along the edges of lakes and canals (Castello, 2008a). Owing to these vulnerabilities and their high economic value, arapaima are among the most overexploited freshwater fishes in South America, with current populations estimated to be ~13% of historical levels (Castello, Stewart, & Arantes, 2011). They are even locally extinct in some regions (Castello, Arantes, McGrath, Stewart, & de Sousa, 2015). Although small-scale fisheries management of arapaima has successfully promoted the local recovery of non-migratory floodplain fishes (Campos-Silva & Peres, 2016; Castello, Viana, Watkins, Pinedo-Vasquez, & Luzadis, 2009; Oviedo & Bursztyn, 2016; Petersen, Brum, Rossoni, Silveira, & Castello, 2016), diverse reproductive traits would introduce the need for more specifically tailored conservation schemes. Protecting floodplain fishes such as arapaima depends on setting an appropriate minimum size of capture and limiting fishing efforts during reproduction, while maintaining critical spawning and nursery habitats.

The main goal of this study was to evaluate length frequencies of harvest and two reproductive traits for arapaima. By comparing data collected for multiple sites in one region with published data for other regions, two null hypotheses were tested: (i) length at first female maturation for arapaima is consistent among sites; and (ii) arapaima nest features do not differ among sites. Measurements were taken during commercial harvest and nest surveys were carried out in the field at several sites in the Lower Amazon. The nest surveys were performed across varying habitat types, arapaima densities, and fishing practices. The length frequencies of harvest were evaluated with respect to the minimum legal size for capture and length at first maturity. These observations were compared with previously published literature. Further recovery of arapaima populations may be hindered if diverse reproductive traits are not accounted for when establishing conservation and management schemes.

2 | METHODS

2.1 | Study Area

Data collection was conducted in the Lower Amazon, near the city of Santarém, Pará State, Brazil (Figure 1). Study sites were located along the whitewater reaches of the Amazon, near its confluence with the Tapajós River. Whitewater floodplains, also called várzea, are characterized by slightly alkaline waters, high primary productivity, high turbidity, resulting from suspended sediment loads, and high aquatic biodiversity and biomass (McClain & Naiman, 2008; Melack & Forsberg, 2001). These floodplains are characterized by cyclically flooding and receding waters that bridge semi-terrestrial zones with permanent aquatic habitats and create a continuous aquatic network at peak flood. In the Lower Amazon, the annual flood pulse reaches



FIGURE 1 Study locations in the Lower Amazon near the city of Santarém, Brazil, with three arapaima (genus *Arapaima*) population density levels: (i) high (Aritapera); (ii) medium (Tapará); and (iii) low (Atuma/Salvação). In order of decreasing arapaima population density, the five fishing communities were: (1) Ilha do São Miguel, (2a) Santa Maria, (2b) Pixuna, (3a) Centro do Aripiri, and (3b) Ilha do Carmo

a low in November/December, with the peak flood pulse averaging approximately 7 m higher in May/June (Goulding, Barthem, & Ferreira, 2003; Junk et al., 2014). Várzea floodplain habitats in the Lower Amazon border the main river channels and contain a complex and constantly changing mosaic of smaller river channels, lakes, swamps, floating vegetation, herbaceous vegetation, shrub, sparse woody vegetation, forest, and agricultural plots. Study sites were located within an area of about 2000 km², creating an oval measuring 70 km at its longest axis and 35 km at its shortest axis. Considering that the natural range of arapaima spans an estimated 2.9 million km², the study area represents less than 0.01% of the overall range of arapaima.

Study sites were selected in five distinct fishing community zones outside formally protected areas on the várzea floodplain. Each community zone has federally recognized boundaries, and community inhabitants work together on community planning and management efforts. These efforts, including arapaima management initiatives, are highly variable in application and execution among the different communities. The five communities or study sites were stratified into three groups based on location and the arapaima population density estimates presented in Castello et al., (2015): high, Aritapera; medium, Tapará; and low, Atuma/Salvação (Figure 1; Table 1).

2.2 | Size at first reproduction for female arapaima

2.2.1 | Sampling

To determine the sizes at which arapaima become reproductively mature, individuals were examined from the commercial harvests between May and November in three floodplain regions (Table 1). In total, 647 arapaima (322 females and 325 males) were sampled during harvests. For each arapaima, the sex was identified, the total length was measured using a flexible tape measure (measured along the dorsum from the tip of the upper jaw to the tip of the caudal fin), and the level of maturity was determined for each female. Arapaima females

TABLE 1 Localities and years for data collection for arapaima (*Arapaima* sp.) reproductive ecology in Lower Amazonian floodplain communities, stratified by arapaima population density

Region	Arapaima density class (no. km ⁻²)		Community	Latitude, Longitude	Observed gonads (years)	Nest surveys (years)
Aritapera	High	(35.5)	Ilha do Sao Miguel	2.101675° S, 54.580984° W	2009, 2012, 2013	2013
Tapará	Medium	(18.79)	Santa Maria	2.352360° S, 54.568706° W	2012, 2014, 2015	–
		(16.89)	Pixuna	2.390578° S, 54.572956° W	2012, 2013, 2015	2014
Atuma	Low	(5.5)	Centro do Aripiri	2.072083° S, 54.993712° W	2012, 2013, 2014	–
Salvação		(1.6)	Ilha do Carmo	2.027986° S, 54.767097° W	2014	2013

have a single functional gonad and are partial spawners (Godinho, Santos, Formagio, & Guimarães-Cruz, 2005). The level of maturity was determined by macroscopic observations of the female gonad and then ranking it on a scale from I to IV (Figure S1), adapted from Lopes and Queiroz, (2009) and Arantes et al., (2010):

- Stage I (immature) – the ovary is elongate, narrow, and pink; no oocytes are visible on the gonadal surface.
- Stage II (maturing) – the ovary is pink or cream, with the presence of visible white oocytes on the gonadal surface; the ovary is slightly swollen and vascularization is more evident, but there is no green, blue, or purple colouration.
- Stage III (mature) – the ovary is large, swollen, rounded, and vascular; some green, blue, or purple colouration may be present in a pink matrix.
- Stage IV (very mature) – the ovary is large, swollen, and rounded in cross section, with complete or near-complete green, blue, or purple colouration; the mature stages included females that recently spawned or 'inactive' adults, because arapaima are partial spawners and never have an empty ovary.

2.2.2 | Data analysis

All statistics were performed in JMP 9.0.1. All analyses for size at first reproduction were executed for pooled data and then stratified into groups based on arapaima population density and location (Figure 1; Table 1; see above). Total length was stratified into 10-cm intervals. To compare sizes of harvested arapaima, length–frequency distributions for males and females were plotted graphically. The gonadal maturity of females was plotted as a proportion of the four maturity stages versus length intervals to visualize the progression of female maturation.

The total length of first sexual maturation (L_{50}) for female arapaima was determined using nonlinear logistic curves. A logistic curve was fitted to the proportion of reproductively mature female arapaima (M_f) by total length (L), using the equation:

$$M_f = 1 / (1 + \exp[-r(L - L_{50})]),$$

where r is the slope of the curve and L_{50} is the mean length at first maturity, or the length where a proportion of 0.5 (or 50%) are reproductively mature. For each region, the consistency in L_{50} between

collection years was evaluated by checking for an overlap in confidence intervals. The overlap of confidence intervals for L_{50} was also used to compare estimates among regions. Finally, findings were compared with available estimates for female arapaima maturity from other areas. Ideally, L_{50} was used as the basis of comparison, but other maturity estimates were considered. For studies that did not calculate L_{50} but presented a total-length frequency distribution of size classes and maturity (Godinho et al., 2005; Guerra Flores, 1980; Hurtado, 1997), L_{50} was calculated following the protocol above after generating a data table by applying the median of each frequency interval for the number of fish in that interval and classifying the specified proportion as mature.

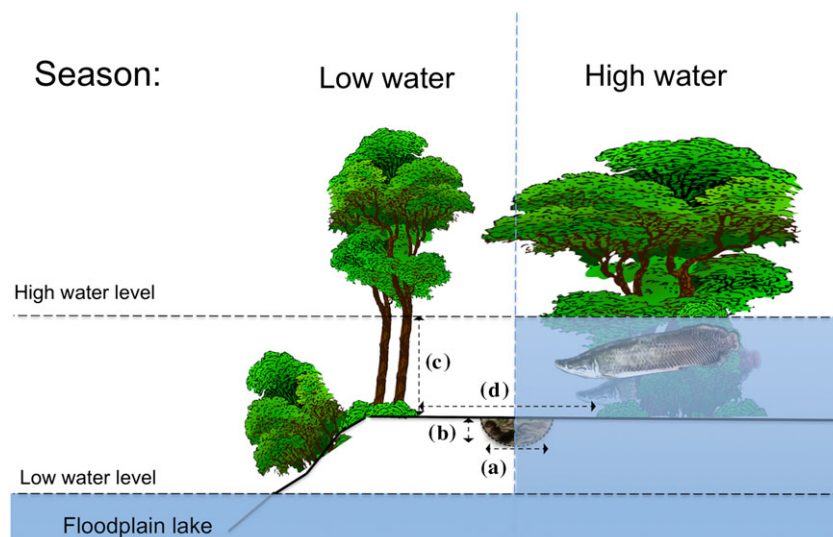
2.3 | Nesting habitat surveys

2.3.1 | Sampling

To identify arapaima nest features, nest surveys were performed in one community zone in each of the three community groups in 2013 or 2014 (Table 1). In each community zone, sampling for arapaima nests was conducted by accompanying expert fishers with an intimate knowledge of arapaima reproductive areas. Surveys were performed by walking transects during the low-water season (in November and December) in habitats adjacent to permanent water bodies that are inundated during high water (Table 1). Transects were conducted on raised banks along the periphery of enduring water bodies, including along the main river channel, smaller canals, lakes, and shallow, semi-enduring lakes, as described by Castello, (2008b). The transects were approximately 30 m in width, starting from the edge of permanent water bodies. The distance travelled during surveys was recorded using a handheld GPS unit.

The following measurements were made for each nest found (Figure 2): (i) nest diameter; (ii) nest depth or height; (iii) height of the last flood relative to nest, determined by water marks on nearby trees and vegetation; (iv) diameter of area around the nest brushed clean (i.e. free of fallen tree leaves and small branches); and (v) a classification of the surrounding habitat. The habitat was classified into one of five Amazon floodplain habitat categories presented in Hess, Melack, Novo, Barbosa, and Gastil, (2003): (i) sparsely vegetated (<10% vegetation cover); (ii) herbaceous (dominated by non-woody plants, with <25% cover by trees or shrubs; herbaceous cover is usually >25% but may be less if herbaceous cover exceeds that of other life forms); (iii) shrub (dominated by shrubs, with individuals or clumps not touching to interlocking; shrub cover is usually >25%); (iv) woodland (dominated by trees with an open canopy

FIGURE 2 *Arapaima* (genus *Arapaima*) often build nests and spawn in floodplain habitat that is flooded during high water, but is accessible on foot during low water. In addition to classifying the surrounding habitat, the following measurements for arapaima nests were standardized: (a) nest diameter; (b) nest depth or height; (c) height of the last flood, as determined by water marks on nearby trees and vegetation; and (d) diameter of area around the nest brushed clean (i.e. free of fallen tree-leaves and small branches)



where tree crowns are not touching, generally forming 25–60% cover, but may be less if tree cover exceeds that of other life forms); and (v) forest (dominated by trees with a closed tree canopy where tree crowns are interlocking, generally forming 60–100% of crown cover).

2.3.2 | Data analysis

To evaluate and compare nest dimensions, descriptive statistics (range, mean, SD) were calculated for nest measurement data stratified by community zone (Figure 2) and region. Measurements of nests from the Central Amazon (Castello, 2008a) and Guyana (Watson et al., 2016; Watson, unpubl. data) were included in all analyses. Observations from captivity (fishes in pond culture) were also presented. The differences among means of each feature were evaluated using Tukey's honestly significant difference (Tukey's HSD) test, a multiple pairwise comparison procedure that identifies which means are significantly different from one another. Multiple linear regressions were used to evaluate the relationship between depth (dependent variable) and diameter (independent variable) for each region. A general linear model with interaction (where depth is the dependent variable and both diameter and region are the interacting independent variables) was used to determine which pairs of regressions were significantly different from one another. Nesting habitat preference was determined by calculating the percentage of nests in each floodplain habitat category.

The relationship between the density of arapaima nests and the density of arapaima was determined as follows. For each area surveyed, the density of arapaima nests (nests km⁻¹) was calculated by dividing the number of nests found by the linear distance travelled during transects. Nest density for each area was plotted against arapaima population density estimates from Castello et al. (2015). To create a more robust relationship, the nest and arapaima densities from the Central Amazon were added to the scatter plot and evaluated with collected data using a linear regression (Castello, 2008b; Castello et al., 2011). For any outliers, the probability that the outlier belongs to the reference population was calculated based on an outlier analysis relative to the linear regression of nest density

versus arapaima density (see Cook & Weisberg, 1982; analysis available in software package STATISTIX 10 for WINDOWS; <http://www.statistix.com>).

3 | RESULTS

3.1 | Size at first female maturity

The estimated total length of a female at first maturation (L_{50}) for combined data for the study area was 149 cm, but significant differences were observed among sites (Figure 3). The 95% confidence intervals for L_{50} at Aritapera – the site of high population density – did not overlap with confidence intervals for either of the other two sites, indicating a highly significant difference (Figure 3). The length at first maturity at Aritapera was ~30 cm less than elsewhere in the study area (139 cm versus 168–169 cm). There was no significant difference between medium- and low-density sites. Compared with other studies, the estimates for L_{50} in the study area are the shortest and among the largest reported for arapaima (Figure 4). The difference in L_{50} estimates for Aritapera and Tapar was consistent between collection years based on non-overlapping confidence intervals, whereas between different years at the same site, the confidence intervals overlapped by more than 50%. An inter-annual comparison was not conducted for Atuma/Salva because of the limited sample size.

The distribution of maturity levels showed that female arapaima gonads began maturing at about 130 cm (stage II, Figure 5). Observations of male and female harvest included a range of size classes from 70 to 217 cm (Figure 5), but the majority were between 100 and 160 cm (mean = 132 cm; SD = 32 cm). Although there was no significant difference among regions, the mean length of arapaima harvested decreased slightly with decreasing arapaima density (region, mean (SD): Aritapera, 134 cm (26 cm); Tapar, 131 cm (35 cm); Atuma/Salva, 126 cm (34 cm)). The largest arapaima harvested were from Tapar, and were 20–30 cm larger than the largest from Aritapera (Figure 5). Based on the government-specified minimum size of capture, ~70% of arapaima were harvested below the legal size limit

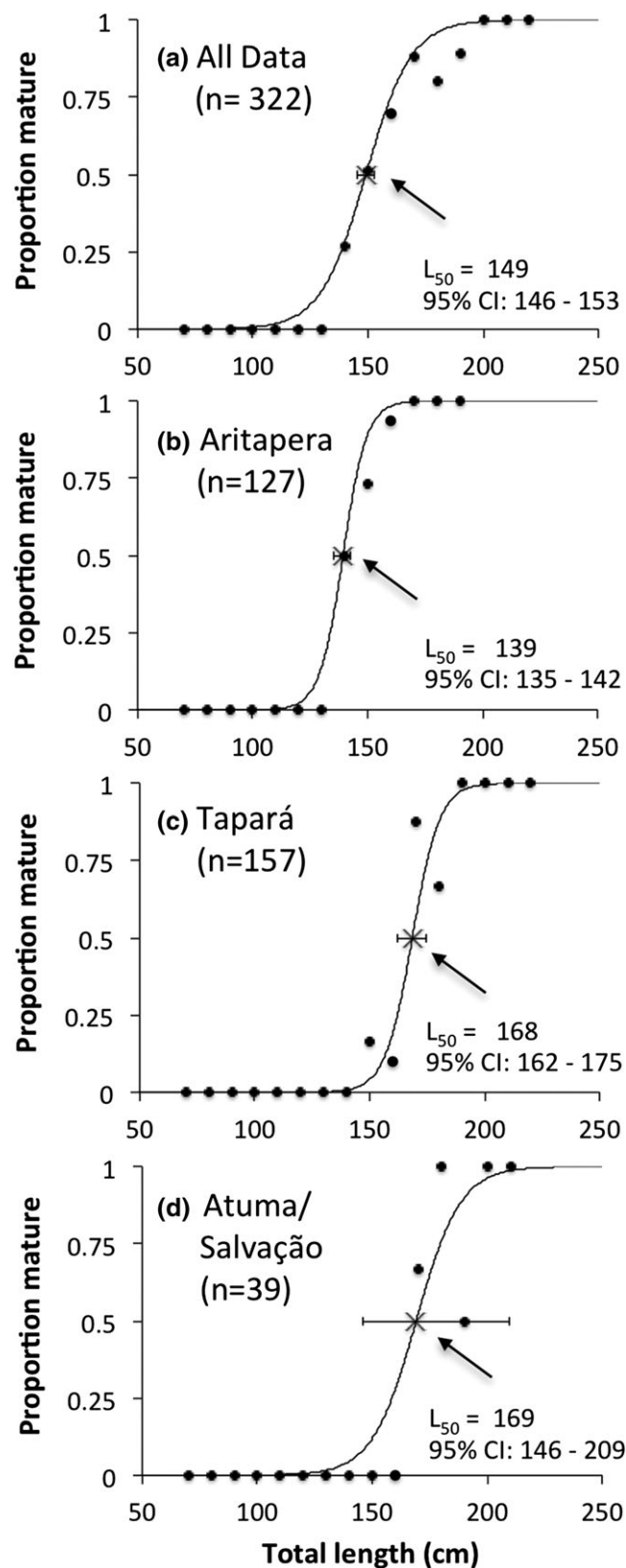


FIGURE 3 Logistic curves and estimated length of females at first maturity (L_{50}) for: (a) all data; (b) Aritapera (high density); (c) Atuma/Salvao (low density); and (d) Tapar (medium density)

of 150 cm, and there was little difference amongst the regions (Aritapera, 66%; Tapar, 71%; Atuma/Salvao, 71%). Using site-based estimates for L_{50} , less than 50% of harvest at Aritapera and more than

80% of harvest at Tapar and Atuma/Salvao were captured below the minimum size at first reproduction (Aritapera, 44%; Tapar, 82%; Atuma/Salvao, 83%).

On average, the harvested female arapaima measured 134 cm, which was slightly but significantly larger than the harvested male arapaima, averaging 129 cm (t ratio = -2.023 ; $P = 0.04$). When separated by region, the average length of female arapaima was also larger than males for each region, but in each case the difference was not significant.

3.2 | Nest surveys

Comparisons of nests from the study locations and other regions show considerable variation among certain features, nesting habitat selection, and the relationship between nest density and arapaima population density. Although no nests were found at the highest arapaima density site of Aritapera, 53 nest depressions in the shape of a cooking pan were found during sampling in the communities of Ilha do Carmo (a low arapaima density region of Atuma/Salvao; $n = 22$) and Pixuna (a medium arapaima density region of Tapar; $n = 31$). For sites in the Lower Amazon, a significant difference was found between the mean values for nest diameter, but not for any other measurements (Table 2). A cleaned area around the nests was observed for 15 of the 53 nests, amounting to 30% of the nests in Salvao and 25% of the nests in Tapar. Compared with other regions, some significant differences were observed among the mean values for nest diameter, depth, volume, depth in the water column, and diameter of cleaned area around the nest (Table 2). For Amazonian sites, there was no significant difference among the available data for the diameter of the cleaned area. Qualitatively, however, two nest types in Guyana had a notable difference in the extent of the cleaned area around the nest (Table 2; Watson et al., 2016). A linear regression showed a positive, and in some cases, a significant relationship between nest depth and diameter. The diameter–depth relationship for one Guyanese morph was significantly different from all others. In the Lower Amazon, at least 90% of nest sites were found below overhanging woody vegetation, with 75% in forest habitat and 16% in woodland habitat, with similar distributions at both sites (Table 2). Only five nests (~9%) were found in open, non-shaded habitat at the edge of a lake or canal. The results for the Lower Amazon closely resemble those for the Central Amazon, where 87% of nests were found in forests. In contrast, however, observations in Guyana revealed that a particular morphology of nests was found almost entirely in open savannah grasslands (Table 2).

After combining nest density observations for the three study sites with three more observations from the Central Amazon (based on Castello, 2008b; Castello et al., 2011), the regression was non-significant ($P = 0.96$). The density of nests at Ilha do Carmo was $0.82 \text{ nests} \cdot \text{km}^{-1}$ and $\sim 2.8 \text{ nests} \cdot \text{km}^{-1}$ at Pixuna. There were no nests found at the highest density site, Aritapera, indicating that this site was a significant outlier ($P < 0.001$). Upon removing this outlier, the regression was positive and significant (Figure 6).

FIGURE 4 Reported estimates for the size of female reproduction in arapaima (genus *Arapaima*) compared with the typical 1.5-m minimum size of capture. Size at first female maturation (L_{50} ; horizontal bars are 95% confidence intervals) was available for the Lower Amazon, Brazil (this study), and the Solimões, Central Amazon, Brazil (Arantes et al., 2010). Using data published in length and maturity frequency tables, L_{50} was calculated for the Tocantins River, Brazil (Godinho et al., 2005), Puerto Nariño, Amazonas State, Brazil (Hurtado, 1997), and Pacaya Samiria National Reserve, Peru (Guerra Flores, 1980). Other observations were reported for the Pacaya River, Peru (Lüling, 1964), and in captivity (Alcantara-Bocanegra, 1990; Bard & Imbiriba, 1986; Fontenele, 1948; Franco-Rojas & Peláez-Rodríguez, 2007)

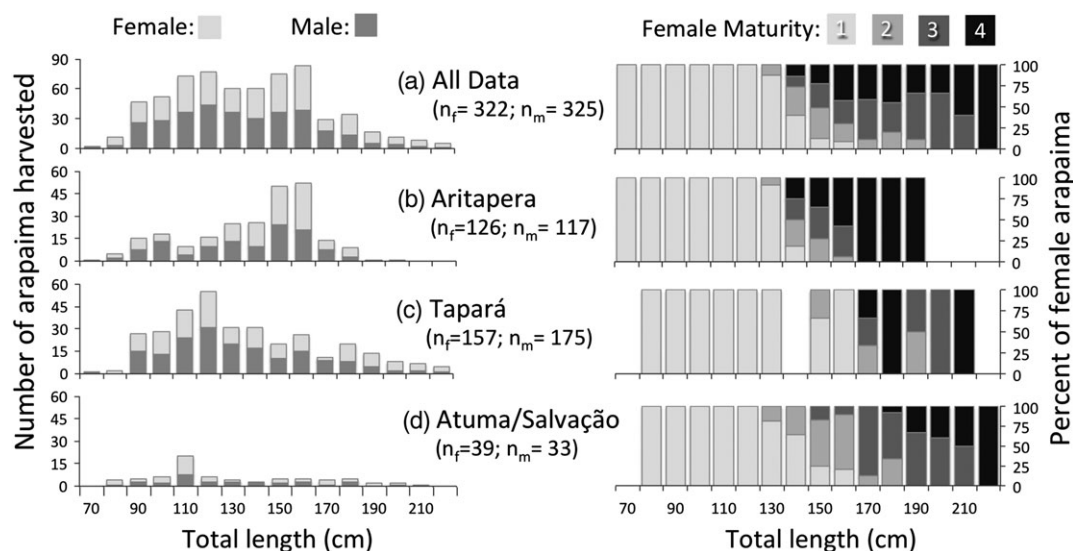
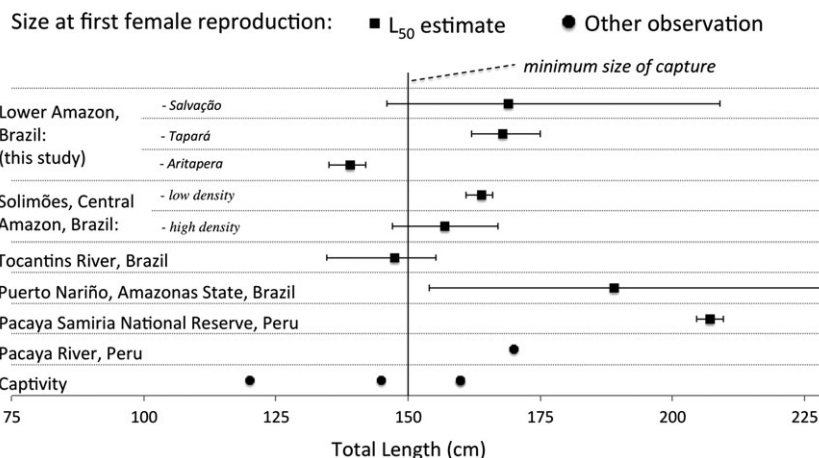


FIGURE 5 Size frequency distributions of arapaima sampled during harvest (left) and the progression of female arapaima maturity (right) for: (a) all data; (b) Aritapera (high population density); (c) Tapará (medium density); and (d) Atuma/Salvação (low density)

4 | DISCUSSION

The results emphasize the diversity in both size at maturation and nests of the genus *Arapaima*. This diversity was observed at various scales, including across the range of the genus and at multiple sites within a relatively small region in the Lower Amazon. Therefore, both null hypotheses were rejected, and it was concluded that: (i) length at first female maturation for arapaima is not consistent among sites; and (ii) arapaima nesting features differ among sites.

4.1 | Length at first maturity

In a relatively small area in the Lower Amazon, representing only 0.01% of the natural range of arapaima, a nearly 30-cm difference was discovered among sites for the size at which females became

reproductive, using L_{50} as an indicator. These were statistically significant differences. Furthermore, the lowest known L_{50} reported for female arapaima to date was recorded (139 cm). The overall variation in L_{50} estimates for arapaima show an even greater interval, spanning nearly 70 cm from 139 cm in the Lower Amazon to 207 cm in the Upper Amazon in Peru. It is important to note that the methods for estimating L_{50} can influence the outcome of the analysis, and it is important to use standardized protocols (Brown-Peterson, Wyanski, Saborido-Rey, Macewicz, & Lowerre-Barbieri, 2011; Núñez & Duponchelle, 2009; e.g. Figure S1). Given the large range of the genus *Arapaima*, however, some reproductive variation should be expected. *Arapaima* occur naturally across two major river basins (the Amazon and the Essequibo), five countries (Brazil, Columbia, Peru, Ecuador, and Guyana), four major wetlands in northern South America, and 11 unique freshwater ecoregions in three freshwater habitat types. Other freshwater, tropical fish genera show variation in reproductive

TABLE 2 Nest feature data for arapaima (genus *Arapaima*) are presented from: Lower Amazon (this study), Central Amazon (Castello, 2008a), Guyana (Watson et al., 2016; Watson, unpubl. data), and captivity (Fontenele, 1948, 1952). The difference amongst means was evaluated using Tukey's HSD test (*). Multiple linear regressions evaluated the diameter–depth relationship for each location and a general linear model with interaction determined which pairs of regressions are significantly different from one another (**). For each regression, the slope (*m*), *y*-intercept (*b*), and significance (*P*) are presented

Location	Nest features													
	Diameter (cm)		Depth (cm)		Height of water (cm)		Diameter of cleaned area (cm)		Diameter-depth regressions			Habitat Description		
	Mean (SD) (range)	*	Mean (SD) (range)	*	Mean (SD) (range)	*	Mean (SD) (range)	*	m	b	p			
(sample size)														
Lower Amazon	Salvação (n = 22)	61.9 (6.7) (50–78)	b	18.4 (4) (12–30)	ab	199.1 (33.6) (130–256)	b	208.6 (108.4) (78–365)	a	0.31	–0.96	0.01	b	- forest: 86% - woodland: 9% - nonvegetated 5%
	Tapará (n = 31)	91.0 (25.1) (55–180)	a	19.1 (4.6) (8–30)	ab	287.2 (65.0) (200–420)	b	2.69 (108.4) (135–480)	a	0.01	18.30	0.79	b	- forest: 74% - woodland: 16% - nonvegetated: 10%
	Aritapera (n = 0)	–		–		–		–		–				–
Central Amazon	Solimões (n = 301)	57.5 (24.2) (12–227)	b	16.0 (7.0) (2–48)	b	434.1 (132.9) (220–800)	a	234.3 (96.5) (50–500)	a	0.12	9.30	< 0.01	b	- woodland and forest: 87%
Guyana	Essequeibo – sharply cut (n = 17)	45.6 (10.8) (26–67)	b	21.3 (6.0) (12–32)	a	186 (± 88.3) (150–450)	b	none	n/a	0.44	1.29	< 0.01	a	- savannah, grassland (except one in woodland)
	Essequeibo – round bottom (n = 4)	99.3 (57.0) (50–174)	a	17.8 (7.2) (14–28.5)	ab	325 (144) (200–450)	ab	Extensive, but not quantified	n/a	0.11	6.64	0.11	b	- openings in forest or woodland
Captivity	Fontenele (1948, 1952) (n = 20 pairs)	20–50	n/a	20	n/a	80–100: 55%, 130–150: 25%, 170–190: 20%	n/a	–	n/a	n/a				- 50% built nests in areas with no floating vegetation present

*Means not connected by the same letters are significantly different ($P \leq 0.05$), based on Tukey's HSD test.

**Regressions not connected by the same letters are significantly different ($P \leq 0.05$), based on a model with interaction followed by Tukey's HSD test.

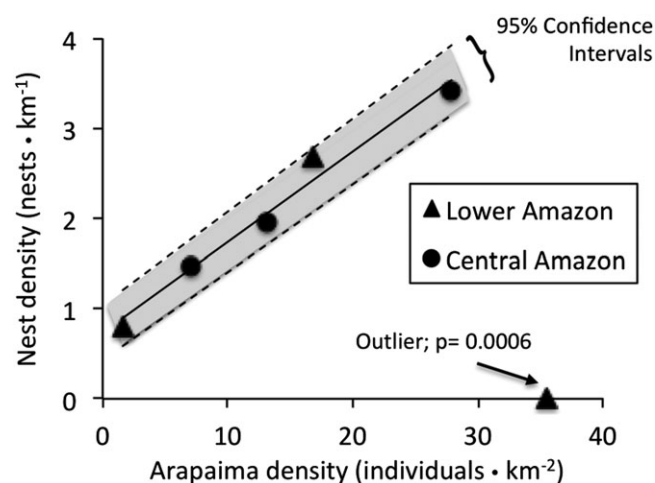


FIGURE 6 The relationship between population densities of arapaima and arapaima nests in: (i) three sites in the Lower Amazon under varying management regimes surveyed in 2014; and (ii) one area in the Central Amazon surveyed over 3 years of varying arapaima population densities (Castello, 2008b; Castello et al., 2011). The relationship is not significant for all data ($R^2 = 0.00$), but is positive and significant after removing the single outlier in the Lower Amazon where no nests were found ($n = 5$; $P = 0.00$; $y = 0.1004x - 0.7363$; $R^2 = 0.98$). The shaded area represents the 95% confidence interval for the simple linear regression relationship after excluding the outlier. The P value represents the probability that the outlier belongs to the reference population, based on an outlier analysis relative to the linear regression of nest density versus arapaima density

strategies (e.g. the genus *Cichla*; Gomiero & Braga, 2004). Even within species, reproductive variation can be observed, resulting from environmental gradients, genetic diversity, and abiotic factors such as variation in habitat or flood pulse patterns (Duponchelle et al., 2015; McDermid, Shuter, & Lester, 2010; Vieira et al., 2009; Zhao, Shuter, & Jackson, 2008). However, because notable variation is not observed in flood-pulse or habitat characteristics in the Lower Amazon study area, where there are anthropogenic pressures from cattle ranching and agricultural practices, they are unlikely to be drivers of the 30-cm difference in size at first maturity for female arapaima in the area. The sites are approximately 30 km apart with no physical barrier between them. Instead, the diversity in size at first maturation in the Lower Amazon could be a result of fishing pressure, fishing gear, or genetic variation. It is possible that high fishing pressure results in lower arapaima density and a larger length at first maturity. For example, relatively high fishing pressure in the 1990s (especially on immature fishes) in the Central Amazon resulted in a lower arapaima density, with sexual maturation at slightly larger sizes and later ages ($L_{50} = 164$ cm and 4–5 years), compared with records for the high population density conditions ($L_{50} = 157$ cm and 3 years) achieved 9 years after implementing management initiatives (i.e. a reduction of 7 cm in L_{50} ; Arantes et al., 2010). Irrespective of the year of data collection in the Lower Amazon, the largest L_{50} is observed for low- and medium- density conditions (~168 cm), and the lowest L_{50} is observed for high-density conditions (139 cm). Nevertheless, as noted above, the mean length of harvested fishes and the percentage of harvested fishes below

150 cm were not significantly different among sites. A similar high percentage of immature fishes being harvested near Santarém was observed in the 1990s (Martinelli & Petrere, 1999).

Second, the difference in maturity might be associated with a notable variation in fishing techniques that exert size-selective fishing pressures. Although the overall proportions of fishes captured in different size classes was not significantly different among sites, at the site with low L_{50} , Aritapera, all fishing is done with baited hook and line, harpoon, or cast net. At all other sites, the same methods are used, frequently with gill nets of various mesh sizes (Figure 5). Different fishing techniques can result in size-selective population shifts (Arantes et al., 2010) and even in shifts in population genetics (Allendorf & Hard, 2009). In addition to a low L_{50} , the maximum length of harvested arapaima at Aritapera, the best-managed site with highest arapaima density in this study (Castello et al., 2015), is 20–30 cm smaller than the largest arapaima harvested at Tapará. In fact, only two of more than 240 arapaima at Aritapera were longer than 180 cm. It is possible that the largest fishes are able to evade fishing, or the availability of prey fish at Aritapera differs from other sites. There is evidence, however, that harpoons and baited hooks are effective at capturing very large arapaima. The differences in both L_{50} and maximum sizes observed in this study may be a result of genetic diversity among populations. In Guyana, Watson et al., (2016) showed substantial genetic variation at small spatial scales, and even sympatry of genetically distinct groups. Similar genetic variability among populations in the study area may correspond to ecological and evolutionary differentiation (i.e. sympatric but distinct groups or species). Although genetic data for arapaima in the Lower Amazon have been collected (Ararape et al., 2013), no known study has explored fine-scale genetic diversity among wild arapaima populations at different sites in the region.

4.2 | Nest features

Contrary to expectations, no nests were found in the site of highest arapaima density in the Lower Amazon (Aritapera, the outlier in Figure 6). This may be a result of disturbance to nests or alternative reproductive strategies producing differences in spawning habitat selection, or even the result of behavioural differences of arapaima at that site. Owing to intensive cattle ranching on Lower Amazon floodplains, it is possible that grazing cattle trampled and obscured the nesting sites. It would be expected, however, that some nests would have been found because arapaima nests were found in other areas with varying densities of grazing cattle and related substrate disturbances. Accounts from local fishers suggested that arapaima from Aritapera reproduce in shallow water along the edge of lakes at the end of the lower water period; thus, nest depressions would only be exposed in the most severely dry years. Similar late dry-season spawning behaviour has been reported for arapaima in Peru (Lüling, 1964). This distinct nesting behaviour corresponds with the aforementioned differences in L_{50} and maximum total length. If some arapaima are spawning at the end of the dry season within lakes, whereas others are spawning in floodplain forest habitats (i.e. outside lakes) after flood waters rise, then such behaviour would result in a

separation of certain spawning adults in both space and time. The testable hypothesis that there could be genetic differentiation involved in such a behavioural dichotomy needs further study.

For the nests measured, the greatest differentiation was observed between sites in Guyana and sites in the Amazon basin (i.e. grouping nesting features in the Central and Lower Amazon). The nest feature that differed most was nest diameter, with significant differences between and within regions, possibly caused by differences in substratum among sites (Muñoz, Van Damme, & Duponchelle, 2006) or from the age structure of each population, with older fishes making larger nests. The length frequency of harvested fishes did not noticeably differ between Taparà and Atuma/Salvação, however (Figure 5). For Amazon basin sites, the area that the arapaima cleared around the nest did not vary in any site or region where it was measured, showing consistency in this behaviour. In contrast, nest sites in Guyana revealed two different behaviours, either with extensive clearing or with no clearing (Watson et al., 2016; Table 2). Although clearing behaviour was only recorded for one-third of the nests in the study area, it is possible that most Amazonian arapaima clear nest sites (Castello, 2008a). They may do this as a defensive adaptation to avoid small predatory fishes eating eggs and larvae (Castello, 2008a). Clearing may not have been observed because nesting habitats in the region are subject to the trampling and overgrazing by cattle that move debris and can obscure the outline of understory vegetation that defines the edge of areas cleared by spawning arapaima. There was some variation between sites and among regions in flood height at nesting sites. It is difficult to say precisely how high the water was when the nest was used, however, because various arapaima could spawn through the flood with gradually rising and subsiding waters. The habitat classification of arapaima nesting sites in the Amazon basin was largely uniform, with nearly 90% found in forest or woody vegetation. In contrast, in Guyana some arapaima spawn in savannah grassland sites devoid of woody vegetation.

4.3 | Conservation implications

This study reveals problems in floodplain fish conservation and management resulting from the frequent harvest of immature arapaima and modification of critical nesting habitat. These threats to arapaima will be further complicated by the consequences of climate-induced changes to water quality and quantity that could affect arapaima reproduction (Frederico, Olden, & Zuanon, 2016). The problem of harvesting immature fish is caused by widespread illegal fishing and inappropriate regulations. The results demonstrated non-compliance with the minimum size of capture in the Lower Amazon, with the majority of harvest, ~70%, falling below the minimum legal limit. Similar non-compliance has been observed in other studies in the Central and Lower Amazon (Castello & Stewart, 2010; Cavole, Arantes, & Castello, 2015; also see Martinelli & Petrere, 1999). In addition, the results show that compliance with the current legal minimum size of capture allows the legal harvest of non-reproductive individuals at most sites (all except Aritapera). This would decrease both the sustainability and the reproductive potential of arapaima populations. In contrast,

when evaluated using estimates for lengths at first maturity, less than half of the harvest in the high-density site was 'undersized', whereas more than 80% was undersized in medium- and low-density sites. There is a need, therefore, to improve the spatial resolution of management and enforcement to ensure that the majority of arapaima harvested, and presumably sold to market, are not reproductively immature.

A further complication is the diversity in lengths at first maturity, both across the range of arapaima (70-cm interval) and even among sites within a region (30-cm interval). This variation presents unique and, to date, unrecognized conservation challenges for arapaima. Although the present conservation and management of arapaima must be conducted using the best available information, despite data deficits, the regulations must eventually be evaluated and adjusted as needed to maximize their effectiveness. Owing to the variability in life-history traits among geographical populations, the application of a uniform minimum size of capture across all arapaima populations is not appropriate, and might result in the extirpation of arapaima populations that have larger sizes or later ages of first reproduction (Castello et al., 2015; Dulvy & Reynolds, 2009). In Peru, for example, preventing the extinction of late-spawning fishes (>2 m) might require extensive no-take reserves with game guards, analogous to what is needed for some large mammals of East Africa. Verifying the continued existence of such fishes in Peru and assuring their conservation should be given high priority. The minimum size of capture either needs to be set conservatively high (i.e. higher than 150 cm) or needs to be evaluated at the population level to determine suitable regulations based on L_{50} estimates. Evaluation at the population level presents conservation challenges in determining and enforcing a variable minimum size of capture at regional and local scales.

This study shows that forested habitat needs to be protected or restored where it has been degraded or lost. Almost all arapaima nests in the Lower Amazon were found in forested or woody habitats, although arapaima at Aritapera appear to be an exception. This corroborates findings in the Central Amazon, where arapaima were found to depend on forested areas to nest and spawn (Castello, 2008a). In addition, arapaima use vegetated areas as nursery grounds (Castello, 2008b; also see Video S1). Deforestation and habitat alterations, such as the overgrazing of vegetation by cattle (Goulding et al., 2003; Renó et al., 2011), can limit the spawning and nursery grounds needed for fish reproduction. This is troubling considering that forests of the Amazonian floodplains continue to be threatened by land-cover changes (Renó et al., 2011).

Although small-scale management initiatives for arapaima have promoted the local recovery of overexploited arapaima populations, these efforts can be hindered by ineffective regulations and the degradation of critical habitats (also see Gurdak, Arantes, Castello, Stewart, & Watson, in press). Modifying and adapting continuing management efforts can improve success and promote continued efforts. Based on the findings, three main recommendations are suggested:

1. set conservative regulatory and enforcement schemes (i.e. minimum size of capture larger than 150 cm) that are evaluated and adjusted as needed to maximize effectiveness;

2. protect and restore forest cover and aquatic macrophytes in the Lower Amazon (and elsewhere) through effective land-use practices; and
3. determine which factors contribute to the significant regional differences in life histories among arapaima populations.

The overall greatest threat to the conservation of arapaima and other floodplain fishes is ignorance of their basic biology.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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