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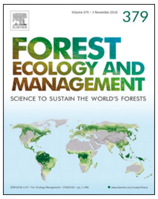

Flipped reducetarianism: A vegan fish subordinated to carnivory by suppression of the flooded forest in the Amazon

Taís Melo[a,*], Gislene Torrente-Vilara[b], Cristhiana Paula Röpke[c]

[a] Laboratório de Ictiologia e Pesca, Universidade Federal de Rondônia, Porto Velho, Rondônia, Brazil
[b] Departamento de Ciências do Mar, Universidade Federal de São Paulo, Santos, São Paulo, Brazil
[c] Departamento de Ciências Pesqueiras e Ciências Biológicas, Universidade Federal do Amazonas, Manaus, Amazonas, Brazil

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ABSTRACT

The effects of dams closure and floodplain forest removal on diet and body condition of a frugivorous migratory fish from the Amazon were evaluated herein. Fish were captured with gillnets in two different environmental conditions: before and after the construction of the Santo Antônio reservoir in Madeira River, preceded by clearing of floodplain forest to mitigate the effects of eutrophication into the run-of-river dam. A total of 493 *Mylossoma duriventre* specimens were accessed and showed a strong shift in diet while body condition did not change after reservoir formation. The vegan diet based on fruits and seed was associated to *Mylossoma duriventre* prior to damming, and replaced by a carnivorous one, mainly based on insects. Our results suggest that dietary plasticity has guaranteed its body condition, at least in the first two years after damming. Cutting off floodplain forest to avoid eutrophication has immediate and direct impacts upon the supply of fruits and seeds for *Mylossoma duriventre*. Still, substitution with insectivorous diet over a frugivorous one, as observed for *Mylossoma duriventre*, may conceal an underlying problem of decreasing the local ichthyochory and floodplain forest maintenance or restoration of *várzea* areas over the time.

1. Introduction

Wetlands are crucial landscape elements due to the high biological diversity, therein and, also to the ecosystem functions and services produced. The cyclic input of nutrients in the aquatic-terrestrial transition zone caused by the seasonal flood pulse, a periodic inundation of lowlands, makes floodplain areas among the most biologically productive and diverse ecosystems on Earth (Junk et al., 1989, 2011; Gregory et al., 1991; Naiman and Décamps, 1997; Tockner and Stanford, 2002; Naiman and Latterell, 2005). Despite their ecological and economical value, wetlands have been lost, degraded, or strongly modified worldwide due to human uses practices, and are disappearing much faster than other kinds of landscape (Vitousek et al., 1997; Olson and Dinersteins, 1998; Revenga et al., 2000; Junk et al., 2013). Moreover, the alteration of flow regimes due to climate changes (Arnell and Gosling, 2013) and hydropower damming of large rivers threaten the ecological integrity of river-floodplain ecosystems around the world (Nilsson and Berggren, 2000; Bunn and Arthington, 2002; Naiman et al., 2002; Kingsford, 2016; Pulles et al., 2016; Winemiller et al., 2016).

In general, flow regulation of large reservoirs eliminates the seasonal flood-pulse and the exchange of nutrients between rivers and their floodplains. The consequence of these processes is a replace of the primary productivity based mostly on the flooded forest by plankton modifying availability of food resources for fishes and other animals, especially fruits and seeds (Junk et al., 1989, 2011; Agostinho et al., 2008). These changes reduce the overall contribution of allochthonous resources but may increase the availability of autochthonous ones (Hahn and Fugi, 2007). As a consequence of such transformations, fish populations that depend on resources from the forest may be strongly reduced or even locally extirpated, or have their diets adjusted to alternative available resources within the new environment. The abrupt change caused by the modification of the flow regime tends to favor generalist species, which have more flexible with their diets and may be able to quickly shift to more abundant resources (Poff and Allan, 1995).

Impoundments also causes the decomposition of organic matter in flooded forest, resulting in eutrophication (Tundisi, 2007). The final stage in the decomposition of vegetation produces an acidic and hypoxic (or even anoxic) environment and, furthermore, stratification of the water column (Fearnside, 1989; Kasper et al., 2014). Hydropower projects attempt to mitigate the effects of eutrophication through the clearing of floodplain forest before filling the reservoir, which provides

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* Corresponding author.
E-mail address: taaismelo@gmail.com (T. Melo).

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Fig. 1. *Mylossoma duriventre* (CP = 13.2 cm) specimen caught on Santo Antônio reservoir on the Madeira River. Photo: Laboratório de Ictiologia e Pesca.

an opportunity to study the effects of floodplain forest removal on the diet of frugivorous fishes.

Although a large number of dams have been constructed around the world, there is a low number of publications considering their impacts on the diet and trophic structure of fish assemblages is rather small, due to scarcity of available data before and after the impacts. In the Neotropical region, changes in the diet of fish species due to construction of dams have been only received attention in recent years (Hahn and Fugi, 2007; Delariva et al., 2013). However, reports considering such changes in fish diets after a run-of-river dams are inexistent in the Amazon basin, the largest wetlands in the world. In this study we focus on the frugivorous serrasalmid fish *Mylossoma duriventre* (Fig. 1), regionally known as “common pacu” as a model to assess the changes in the diet, body size, and body condition after the construction of a large run-of-river dam in Madeira River Basin, Brazilian Amazon. Although most species of pacus (Myleinae) do not have a strictly herbivorous diet (Araújo-Lima et al., 1986; Cella-Ribeiro et al., 2016), *Mylossoma duriventre* is described as a strongly frugivorous species that depends on allochthonous food items to survive and complete its reproductive cycle. Moreover, it was one of the most abundant fish captured both before (pre-UHE) and after (post-UHE) the construction of the Santo Antônio run-of-river dam (UHE Santo Antônio). Considering the persistence and abundance of *Mylossoma duriventre* after the construction of the UHE Santo Antônio, we expect that the “common pacu” will show qualitative and quantitative changes in its diet after the formation of the dam’s reservoir and the changes in floodplain forest cover and flood pulse dynamics, with consequent changes in body condition.

2. Material and methods

2.1. Study area

The Madeira River is a tropical white-water river (Sioli, 1964, 1984; Junk et al., 2011), and the largest tributary of the Amazon Basin, recognized for its extensive floodplain areas (regionally called *várzea*) in its lowermost reaches (Goulding, 1979, 1980; Queiroz et al., 2013). The study site included a river length of approximately 20 km located in the rapids stretch where floodplains were very scarce and restricted to the mouth of some tributaries (Fig. 2; Queiroz et al., 2013). Before the damming by the UHE Santo Antonio the river exhibited a seasonal flood pulse with a low water phase between May and October and a flooding phase between November and April. High discharges of up to 45.000 m^3/s were recorded during especially strong floods (Torrente-Vilara et al., 2011; Cella-Ribeiro et al., 2017). The reservoir area, exposed to natural flooding in the sampled section used to be about 164 km^2 of wetland (IBAMA, 2007), covered by 91.68% of primary forest, 4.34% of secondary forest, 1.19% “capoeira”, and 2.79% of pasture (SEDAM, 2013). A mitigation measure to curtail the eutrophication of reservoirs and greenhouse-gas emissions (Fearnside, 1989; Fearnside and Pueyo, 2012) resulting from the decomposition of permanently submerged lowland forest is clearing the vegetation before the formation of the reservoir. The cut off of the forest that would be flooded by the UHE Santo Antonio was finished in August 2011, and the reservoir was filled in September 2011. The area permanently flooded by the UHE Santo Antonio was 271 km^2, which includes all the previous wetlands of this area and a percentage of upland forests (Fearnside, 2014; Cella-Ribeiro et al., 2017). The original forest cover present in the Madeira River rapids stretch inventoried before the permanent inundation included at least 120 tree species (SEDAM, 2013; Table S1).

Five sampling sites were established in the studied river stretch: Jatuarana Creek (JAT; 08°49′52.1″W; 64°02′43.8"S) and the Jaciparaná River (JAC; 09°17′ 01.0″W; 64°23.1′57.3"S) before the river damming, and three sites were added within the reservoir area after damming: upstream (RSA; 09°09′49.6″W; 64°29′ 52.7“S), midstream (RSM; 09°07′1.1″W; 64°18′54.1″S) and downstream (RSB; 08°51′53.4″W; 64°03′19.0″S; Fig. 2).

2.2. Data collection

Specimens of *Mylossoma duriventre* were sampled during 23 expeditions carried out monthly before damming (pre-UHE phase) from November 2008 to August 2011, and 12 bimonthly expeditions after damming (post-UHE phase) from October 2011 to August 2013. A set of 13 gill nets (each gillnet with 10 m in length and 1.5–3.5 m in height) totaling an area of 431 m^2 were used at each sampling event in pre- and post-UHE phases at the JAT and JAC sampling sites. In the post-UHE phase the sampling sites upstream (RSA), midstream (RSM) and downstream (RSB) were sampled with two sets of 11 gillnets (each gillnet with 25 m in length and 1.5–3.5 m in height), totaling an area of 1097 m^2. Despite the differences in sampling effort, each data set represents a sample of the populations presented in the pre and post-UHE phases. Captured fishes were euthanized in an ice bath and transported in cooler boxes with ice to the laboratory. Each specimen of *Mylossoma duriventre* was measured (standard length – SL, cm), weighed (total fresh weigh – TW, grams) and had their stomach preserved in 70% ethanol. Subsequently, the stomach fullness was estimated, and the stomach contents identified using an optical stereomicroscope.

Feeding activity was estimated by stomach fullness on a scale from 0 to 3 (Hahn et al., 1999) considering the amount of food filling the stomach: 0 (empty), 1 (< 25%), 2 (25–75%) and 3 (> 75%). The food spectrum was determined by grouping food items into six categories: insects, algae, zooplankton, seeds, fruits and other vascular plants parts (leaves, flowers and twigs). Food items were measured for relative volume (VO%: visually estimated proportion of each item, considering the total volume of the items as 100%; Goulding et al., 1988) and relative frequency (FO: occurrence of the item in relation to the total number of stomachs with food; Hyslop, 1980).

2.3. Data analysis

The methods of relative volume (VO%) and relative frequency (FO) were combined in the alimentary index IAi (Kawakami and Vazzoler, 1980), which values range from 0 to 1 resulting from the equation: $IAi = \frac{FixVi}{\Sigma FixVi}$, where: i = the specific food item; Fi = relative frequency of occurrence of the item i; Vi = relative volume of the item i. The values obtained were then multiplied by 100 in order to describe de diet in terms of percentage.

Determination of the species’ feeding habits in pre- and post-UHE periods was based on the IAi index, considering the items of greater proportion in the food spectrum (IAi > 70%). A histogram of frequency of occurrence by food items for pre- and post-UHE was plotted. The relative body condition (Kn) of *M. duriventre* was calculated following LeCren (1951). Differences in the degree of stomach fullness and

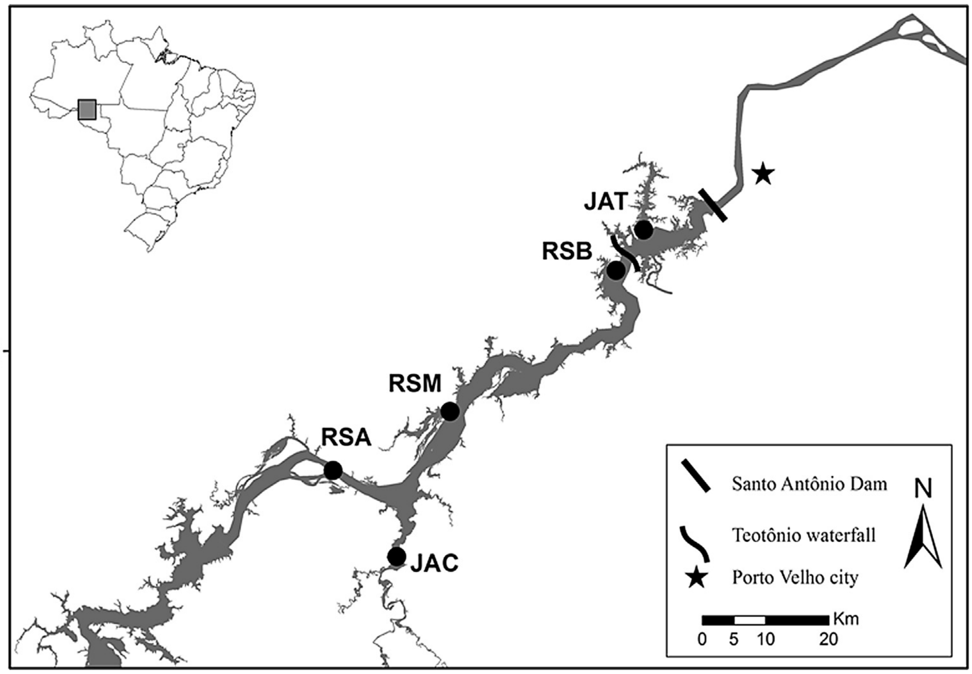

Fig. 2. Map of area under direct influence of the UHE Santo Antônio on the Madeira River. Sampling sites pre-UHE - JAC: Jaciparaná River; JAT: Jatuarana Creek; Sampling sites post-UHE - High portions (RSA), medium (RSM) and low (RSB) of UHE Santo Antônio. Map: Ariana Cella-Ribeiro.

body condition (Kn) between pre- and post-UHE were tested using a Mann-Whitney *U* test. Once changes in the diet could be a consequence of changes in population size structure, differences in the frequency of individuals by size classes were tested using a Kolmogorov-Smirnov test (Birnbaum and Tingey, 1951, Conover, 1971, Durbin, 1973, Marsaglia et al., 2003). Significant differences were considered regarding $P < 0.05$. Statistical analyses were performed using the *R* software and vegan package (R Project – R., 2013).

3. Results

A total of 172 specimens of *Mylossoma duriventre* were captured during the pre-UHE and 321 in the post-UHE phases. The smallest and largest specimens captured in the pre- and post-UHE had similar sizes (8.0 and 8.2 cm; 27.0 and 27.5 cm, respectively). Most specimens (70% of total) had sizes between 12.0 and 16.0 cm in both pre- and post-UHE periods, with no significant changes detected in their mean size ($t_{calculated} = 0.004$; $t_{tabulated(0.05)} = 3.25$; Fig. 3) or frequency of size distribution ($D_m = 0.5$; $P = 0.1641$). Similar result was obtained for the comparison of *M. duriventre* mean body condition (pre-UHE: $Kn = 2.96$; post-UHE: $Kn = 3.22$; $t = -1.25$, $P > 0.05$).

The feeding activity represented by relative frequency of stomach fullness classes was similar between pre- and post-UHE periods: 44% and 39% for GR = 0; 34.7% and 36.4% for GR = 1; 13.5% and 15.1% for GR = 2, and 7.8% and 9.7% for GR = 3, respectively. The mean feeding activity index also did not differ between pre- and post-UHE phases (pre-UHE = 0.49; post-UHE = 0.58, $U = 1.65$, $P > 0.05$). However, diet composition showed a marked change. During the pre-UHE period the most common food items consumed by *M. duriventre* were of vegetal origin from floodplain (IAi = 97.65%), mainly fruits (IAi = 50%), seeds (IAi = 41.70%), leaves and flowers (IAi = 5.42%); insects had a minor representation (IAi = 2.35%) (Fig. 4). These proportions were similar in the high and low water season (Table S2). However, in the post-UHE period food items from higher plants were reduced to about 30%; the consumption of fruits and seeds decreased to IAi = 0.33% and 13.86%, respectively, while leaves and flowers increased to 17% of the diet. On the other hand, in post-UHE period *M. duriventre* increased the consumption of aquatic and terrestrial insects (IAi = 55.02%) and incorporated two previously unrecorded food items in its diet: algae (IAi = 13.54%) and zooplankton (IAi = 0.004%) (Fig. 4).

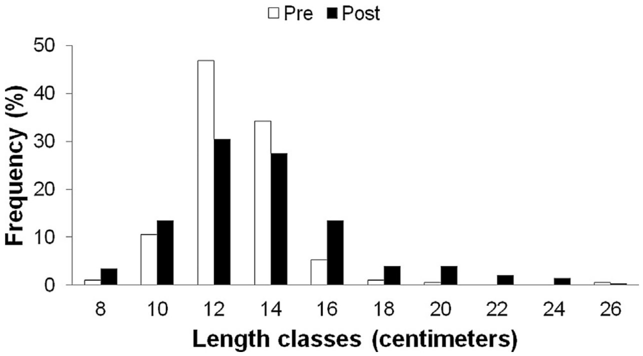

Fig. 3. Length class (SL cm) frequency (%) of *Mylossoma duriventre* captured before (pre-UHE) and after (post-UHE) the construction of UHE Santo Antônio on the Madeira River.

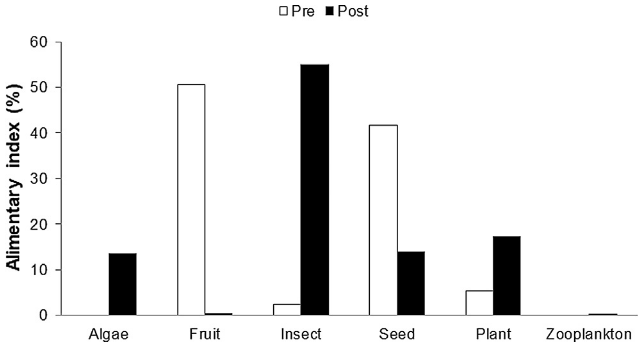

Fig. 4. Alimentary Index (IAI) of food items consumed by *Mylossoma duriventre* before (pre-UHE) and after (post-UHE) construction of UHE Santo Antônio, on the Madeira River.

4. Discussion

Our findings suggest that *Mylossoma duriventre* has a high dietary plasticity, as the fishes altered their frugivorous diet to an insectivorous one while maintaining their body size and condition. The use of alternative food resources did not result in loss of storage energy, preserving the resident population in the Santo Antônio reservoir after two years of the closure of the dam. Dietary plasticity has been reported for several freshwater fish species such as *Astyanax taeniatus* (Manna et al., 2012), and four species of small Characidae species (Fiori et al., 2016) under damming situations. However, these were already generalist species, and not highly or directly dependent on the riparian vegetation.

Previous studies have shown that although species of Myleinae (pacus and relatives) are essentially herbivorous, they are able to feed on insects as a main food source during periods of low availability of plants items, mainly during the low water seasons in floodplains (Correa and Winemiller, 2014). For *M. duriventre,* dietary changes from fruits and seeds to insects (terrestrial ones) were already recorded by Claro et al. (2004) and also related to flooded forest availability around the sampled lakes along the Amazon River mainstem. Nevertheless, most of these studies reporting diet changes are related to seasonal condition, while no previous study has accessed the effects of removing a large portion of a floodplain forest for hydropower damming purposes as reported here. The observed adjustments on *M. duriventre* diet likely reflect the marked changes in food availability in the aquatic environment as a consequence of riparian forest clearing, and hydrodynamic alteration by the formation of the hydroelectric reservoir (Hahn and Fugi, 2007). This hypothesis is corroborated by the fact that *M. duriventre* also fed on fruits and seeds (although less intensely) during low water periods during the pre-UHE phase. Competitive interactions with others frugivorous species resulting in diet changes due to scarcity of resource availability after river damming may not explain our results, since its congeneric species *Mylossoma aureum* was the only frugivorous species detected in this stretch of the Madeira River among more than 70 species (Cella-Ribeiro et al., 2016). Moreover, there are evidences that *M. aureum* also changed its diet after the environmental changes resulting from the UHE construction (data not shown due to low sample size specially after the closure of the dam; Cella-Ribeiro et al., 2017). Although some omnivorous fishes also fed on fruits, most of them reduced in abundance after the closure of the dam, such as the driftwood catfish *Auchenipterichthys thoracathus* (Cella-Ribeiro et al., 2017). Under natural conditions river-floodplain systems periodically incorporate allochthonous food resources from flooded forests (Junk et al., 1989, 2011; Junk and Wantzen, 2004). This organic matter input, associated with the increased environmental heterogeneity created by the flood pulse dynamics, is responsible for the availability of major terrestrial food items to the aquatic fauna. In the cases of damming, there is a change on the physical structure of the habitat, thus affecting the quantity and quality of food resources. Apart from habitat changes, the removal of large individuals by fisheries may also be responsible for changes in the diet of frugivorous fish populations (Correa et al., 2015, 2016; Pereira and Galetti, 2015). Such changes occur because larger fish are able to fed on a higher diversity of plants and a greater range of seed sizes when compared to smaller individuals (Correa et al., 2015). In fact, fisheries data from the Madeira River showed evidences of overfishing as a decrease on the mean body size of *M. duriventre* and other species of pacus (Myleinae) from 1997 to 2004 (Doria and Lima, 2008). However, this hypothesis does not seems plausible once there were no evidences of changes in the size frequency distribution of *M. duriventre* between pre- and post-UHE phases.

Frugivorous migratory fishes are important agents of seeds dispersion for floodplain plants (Galetti et al., 2008; Anderson et al., 2009; Silveira and Weiss, 2014; Boedeltje et al., 2015; Correa et al., 2016), and both riparian deforestation and environmental changes resulting from dams' constructions threatens these complex floodplain systems. The scarcity of studies on the viability of seeds consumed by frugivorous fish makes it difficult to access the importance of *M. duriventre* as a disperser of floodplain plant species. However, Goulding, (1979) reported that small specimens of *Mylossoma* tend to grind seeds or fruits consumed, which highlight the importance of maintaining large individuals of frugivorous pacus (Myleinae) for an effective ichthyochory. Many authors revealed that the larger the individual fish, greater its potential to eliminate viable seeds (Kubitzki and Ziburski, 1994; Galetti et al., 2008; Anderson et al., 2009, 2011; Correa et al., 2015, 2016), though smaller specimens also can be great seeds dispersers (Silveira and Weiss, 2014).

Worldwide, approximately 275 species of fishes consume fruits and disperse seeds in freshwaters (Anderson et al., 2009; Horn et al., 2011; Yule et al., 2016). Of these, at least 150 inhabit South American wetlands (Horn et al., 2011) and disperse the seeds of over 500 plant species (Correa et al., 2015). Plants are sessile organisms and most seeds move short distances (zero to a few tens of metres) depending on agents to disperse away from their maternal trees (Howe and Smallwood, 1982; Sugiyama et al., 2018) to increase offspring survival (Janzen et al., 1976; Connell, 1971). Fruiting is synchronized with annual flooding and many seeds have adaptations that allow dispersal by fishes (Kubitzki and Ziburski, 1994; Chick et al., 2003; Mannheimer et al., 2003; Maia et al., 2007; Anderson et al., 2009; Ferreira et al., 2010; Correa et al., 2015; Yule et al., 2016). The migratory "common pacu" *M. duriventre* seems to potential disperse seeds of at least 15 species in the Madeira River rapids stretch, including *Paullinia* sp. (Sapindaceae), *Amanoa* sp. (Euphorbiaceae), *Ficus* sp. and *Cecropia* whose seeds was reported as ingested whole since decades ago (Goulding, 1979, 1980). However, *M. duriventre* stomach contents analyze in our samples showed that most seeds were broken. Anyway, few seeds can disperse and guarantee gene flux among populations in flooded forest along the rivers. Similarly, analysis of the stomach content of *Triportheus nematurus* (Characidae), from Pantanal, showed that 64% of all seeds of *Banara arguta* consumed were fragmented (Yule et al., 2016). Experimental germination of a few whole seeds showed 80% of success, suggesting *T. nematurus* as a seed disperser also (Yule et al., 2016). *Colossoma macropomum* and *Piaractus brachypomus*, possibly two of the major Neotropical frugivorous fishes, can disperse seeds of up to 35% of the plant species consumed, pointing out the effective seed dispersing by fish in South America (Anderson et al., 2009) even when a percentage of seed is lost when chewed by fish.

After cutting off the floodplain forest and the formation of the UHE Santo Antônio reservoir, the reduction in the current velocity (mainly at the periphery of the flooded area), the consequent sediment deposition and increase in water transparency may have contributed to an increased biological productivity and zooplankton availability, which was incorporated in the diet of *M. duriventre*. As a seasonal migratory species, *M. duriventre* depends on the effective assimilation of variably available food resources and energy storage that may guarantee its reproductive success in the newly formed environment (the UHE's reservoir). However, the persistence of an apparently healthy population of *M. duriventre* in the reservoir area in the absence of a seasonally available floodplain forest in the long run still awaits confirmation. To measure the species colonization success in the reservoir area without the regulating force of a predictable flood pulse it would be necessary to analyze bio-ecological attributes of the population on a time scale equivalent to several generations of the species (life cycle suggested by us about 4 to 6 years based on our personal observation), and perhaps between 15 and 20 years.

The present study has shown that *Mylossoma duriventre*, a frugivorous and commercially important species in Amazon lowlands seems to have been able to persist in the first years after the construction of a large hydroelectric dam in Madeira River. However, it has changed its feeding habits from a vegan to a carnivorous diet, which may impair its potential contribution as a seed disperser of floodplain forest plants. This example indicates that the conservation of several commercially important fishes that inhabits the floodplains of Madeira River strongly depends on the conservation of large areas of seasonally flooded forests that provides food and shelter throughout the life cycles of those organisms. Moreover, the proper ecological functioning of the floodplains can only be maintained if the controlling force of the seasonal flood pulse is maintained, warranting access to basic resources and providing the environmental dynamics that allow fundamental ecosystem services such as hydrochoric and ichthyochoric dispersion of flooded forest seeds. In this sense, alternative arrangements for future hydroelectric enterprises that consider the maintenance of a considerable portion of the riparian forests while employing operation rules that maintain seasonal and predictable water level changes in the reservoir area should be pursued. Those procedures would help preserving the river's longitudinal connection for the sake of its highly diverse amphibious forests and fishes of the Amazon basin.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2018.12.050.

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