Structure and composition of ichthyofauna associated with cage fish farming and compared to a control area after severe drought in a Neotropical reservoir

Aymar Orlandi-Neto¹, Rafael Vieira Amorim², Rosilene Luciana Delariva³, Antonio Fernando Monteiro Camargo², Rosicleire Veríssimo-Silveira⁴ and Igor Paiva Ramos¹,⁴

In 2014, an atypical drought in Southeast Brazil drastically reduced the water level in several reservoirs. We investigated the effects of this drought and the subsequent flood period on the attributes of ichthyofauna in an aquaculture and in a control area. Fish were collected bimonthly between 2014 and 2015 (drought) and 2016 (wet), using gill nets in the two sample areas in the Ilha Solteira reservoir, Upper Paraná River basin, Brazil. We compared ichthyofauna attributes between the drought and wet seasons in each area and between areas within each season. In the aquaculture area, the assemblages showed similar characteristics between the seasons. By contrast, the control area varied between seasons, with greater species richness, Shannon diversity, species evenness, and less β diversity in the wet season. Comparisons between areas in each season showed higher abundance in the fish farm within the drought season. Changes in structure and composition in the control area are possibly associated with new areas and resources made available by the flooding of marginal areas during the wet season. We inferred that the effect of the flood on the aquaculture community was attenuated by the continuous habitat structure such as shelters and food provided by the enterprise.

Keywords: Diversity, Ilha Solteira reservoir, Invasive species, Upper Paraná River, Water crisis.

¹Universidade Estadual Paulista (UNESP), Instituto de Biociências, Botucatu, Programa de Pós-graduação em Ciências Biológicas (Zoologia), R. Prof. Dr. Antônio Celso Wagner Zanin, s/n, 18618-689 Botucatu, SP, Brazil. aymar.orlandi@unesp.br (corresponding author).
²Universidade Estadual Paulista (UNESP), Centro de Aquicultura da UNESP, Jaboticabal, Programa de Pós-graduação em Aquicultura, Via de Acesso Professor Paulo Donato Castellane, s/n, 14884-900 Jaboticabal, SP, Brazil. (RVA) rafa.amorimm@hotmail.com, (AFMC) antoniofmcamargo@gmail.com.
³Universidade Estadual do Oeste do Paraná (UNIOESTE), Centro de Ciências Biológicas e da Saúde, Programa de Pós-graduação em Conservação e Manejo de Recursos Naturais, R. Universitária, 2069, 85819-110 Cascavel, PR, Brazil. rosilene.delariva@hotmail.com.
⁴Universidade Estadual Paulista (UNESP), Faculdade de Engenharia, Ilha Solteira, Departamento de Biologia e Zootecnia, R. Monção, 226, 15385-000 Ilha Solteira, SP, Brazil. (RVS) rosicleire.verissimo@unesp.br, (IPR) igor.paiva.ramos@gmail.com.
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Em 2014 um evento de seca atípica no sudeste brasileiro diminuiu drasticamente o nível da água em diversos reservatórios. Nós investigamos os efeitos dessa seca, e seu subsequente período de cheia sobre atributos da ictiofauna em uma área aquícola e uma área controle. Os peixes foram coletados bimestralmente entre 2014 a 2015 (seca) e 2016 (cheia), usando redes de espera nas duas áreas amostrais no reservatório de Ilha Solteira, bacia do alto rio Paraná, Brasil. Comparamos atributos da ictiofauna entre os períodos de seca e cheia em cada área e entre as áreas dentro de cada período. Na área aquícola, verificou-se similaridade das assembleias entre os períodos. Em contraste, a área controle apresentou variação entre os períodos, com maior riqueza, diversidade Shannon, equitabilidade e menor diversidade β no período de cheia. Comparações entre áreas em cada período, mostraram maior abundância na piscicultura no período de seca. As mudanças na estrutura e composição na área controle possivelmente está associada as novas áreas e recursos disponibilizados pela inundação de áreas marginais no período de cheia. Infere-se que o efeito da cheia na comunidade da área aquícola foi atenuado pela continua estrutura de habitat, como abrigos e ração fornecidos pelo empreendimento.

Palavras-chave: Alto rio Paraná, Crise hídrica, Diversidade, Espécies invasoras, Reservatório de Ilha Solteira.

INTRODUCTION

The construction of reservoirs causes changes in the physical, chemical, geomorphological, and hydrological conditions of rivers, transforming lotic ecosystems into lentic ones (Agostinho et al., 2007, 2016). These changes in environmental conditions tend to modify native species richness and abundance, decreasing community resistance and facilitating introduction or invasion by non-native fish species (Pelicice et al., 2014; Ruaro et al., 2020). Reservoirs are present in the main river basins in Brazil, and the principal purpose is the production of electricity, however, among ours the use multiple, the aquaculture activities have drawn the attention of researchers about their possible effects on the structure of ichthyofauna (Daga et al., 2015; Agostinho et al., 2016; Nobile et al., 2020). A trend toward the replacement of extractive fisheries by aquaculture has been conducted under the argument of the decrease of natural fish stocks and the increase in demand for fish consumption (FAO, 2016). In Brazil, aquaculture can occupy 1% of the surface of a reservoir, but there are concerns about this regulation due to its potential effects on ecosystems (Nobile et al., 2020). In 2020, there was a 4.3% increase in production from Brazilian fish farming compared to 2019, which recorded 551.9 thousand tons of fish. Oreochromis niloticus (Linnaeus, 1758) was the most cultivated species, with 62.3% of the total fish produced or 343.6 thousand tons (IBGE, 2020).

Among the aquaculture industry activities in artificial reservoirs in Brazil, cage fish farming systems stand out. In these systems, there is a continuous input of organic matter and energy in the form of feed, up to 18% of which can be introduced into the aquatic ecosystem in the form of unconsumed feed remains (Montanhini-Neto,
Ostrensky, 2015). The introduction of this matter and of allochthonous energy devoid of this activity contributes locally to changes in the structure of the fish fauna. Such changes have been reported in relation to fish species abundance and richness around the fish farming activity. For abundance, generally, the fish farm increases the wild species abundance (Barrett et al., 2019), however, patterns of the effect of fish farm on the species richness are still unclear. In some studies, an increase in species richness was observed (Barrett et al., 2019; Pereira et al., 2019) and in others, a reduction (Nobile et al., 2018). Fish farming can also act as a source of introduction of non-native species (Britton, Orsi, 2012; Ortega et al., 2015; Ruaro et al., 2020) and favor generalist species (Ramos et al., 2013; Nobile et al., 2018), contributing to fish faunal homogenization processes (Pelicice et al., 2014; Daga et al., 2015; Bezerra et al., 2019).

Besides to aquaculture activities, qualitative and quantitative environmental factors can influence the structure of the fish fauna in reservoirs, such as depth, width, flow, shelter, and resources, associated with climatological/hydrological changes (Agostinho et al., 2007; Bond et al., 2008; Rolls et al., 2016). In Neotropical reservoirs, inter annual or seasonal effects of drastic reduction or rise in the water level in a hydroelectric reservoir are usually avoided or minimized by operation and management in the dam (Gunkel et al., 2018). However, events such as atypical floods and droughts strongly affect habitat and aquatic biota structures in these environments (Lytle, Poff, 2004). Periods of lower water level can favor the dominance of a few species, decreasing fish species richness and diversity (Chessman, 2013; Freitas et al., 2013). Periods of higher water levels allow expansion of the flooded area and greater availability of habitats (Miranda, 2001). This incorporation of new habitats and resources can attract non-resident species, with a consequent increase in species richness and local diversity (Lowe-Mcconnell, 1999; Agostinho et al., 2001, 2016). However, some studies that investigated the similarity among fish assemblage under hydrological effects showed an increase in β diversity during seasons with a lower water level as a result of an increase in species replacement due to greater habitat fragmentation or less connectivity when compared to flooding seasons (Thomaz et al., 2007; Rolls et al., 2016).

An atypical drought recorded during the years 2014 to 2015 in Southeast Brazil caused numerous consequences for urban and rural supply and electricity generation (Coelho, 2016; Hunt et al., 2018). In addition, losses for artisanal fisheries and aquaculture were recorded (Galvão, Bermann, 2015). The few information on the effects of events of droughts and floods in freshwater aquaculture areas refers to productivity and on cultivated fish (Ahmed, Diana, 2016; Ahmed et al., 2019). The scientific production on atypical hydrological events in the aquatic biota in areas close to fish cage systems has not been explored and elucidated. However, the expected of increasing the severity of droughts and aridification in many parts of the world (Park et al., 2018) and the expansion of the cage farms placed in reservoirs in Brazil (Nobile et al., 2020), alert to the necessity and relevance of research in these terms for wildlife management under future extreme hydrological events.

Here we aimed to investigate the structure and composition of the ichthyofauna in an aquaculture area (cage fish farming system) under the effect of an atypical hydrological event due to a severe drought that occurred between 2014 and 2015 and the subsequent rainy season (2016). We hypothesized that the change in the water level has a reduced effect on the ichthyofauna in the aquaculture area compared to the area without this
activity. More specifically, we predict that the effects of the flood on the ichthyofauna are attenuate in the fish farming area, that is, little or no change in the abundance, richness, diversity, evenness, β diversity, and composition of the ichthyofauna between the drought and wet season. Considering that cage fish farming can locally influence fish species abundance by the attraction and aggregation of fish near the cages (Nobile et al., 2018; Barrett et al., 2019; Pereira et al., 2019), we also hypothesized that the fish farming area promoted changes in the structure of the ichthyofauna. Thereby, we expected variation in taxonomic attributes between areas, with higher abundance in aquaculture area for both seasons.

MATERIAL AND METHODS

Study area. The Ilha Solteira reservoir is an accumulation reservoir formed in 1978 by the Paraná River in the region of the Upper Paraná River, Brazil. It has an average depth of 17.6 m, a maximum volume of 21.06 x 10⁹ m³, a basin area of 1,195 km², and a residence time of 46.7 days (Garcia et al., 2015). The sample areas were: one under the influence of a cage fish farming system (fish farm; 20°02'30.54"S 50°55'59.65"W) and one in a location approximately 10 km upstream with similar physiographic characteristics, free from the influence of cage fish farming systems (control; 20°00'13.71"S 50°51'58.94"W) (Fig. 1). Both areas have an average depth of 9 meters, similar elevation (335–350 m) and their margins with agricultural and livestock activities. In 2014 and 2015, there was a significant rainfall deficit in several regions of Brazil, and the state of São Paulo experienced one of the largest droughts ever recorded (Coelho et al., 2016), with historical decreases in water flow, volume (Hunt et al., 2018), and quota of the Ilha Solteira reservoir (ONS, 2018; Fig. 2).

FIGURE 1 | Map of South America showing the Ilha Solteira reservoir, with an indication of the sample areas (black circles). Adapted from Kliemann et al. (2018).
Collection of biological material. Samples were collected bimonthly during the drought (quota below 323 m; December/2014 to October/2015) and wet (quota above 323 m; February to December/2016) seasons, using gill nets of different sizes (3, 4, 5, 6, 7, 8, 10, 12, and 14 cm between non-adjacent knots), set close to the margin or cages (up to 30 m from margin) in the fish farm and control areas between 5:00 p.m. and 6:00 a.m. The collected specimens were identified (Britski et al., 1999; Graça, Pavanelli, 2007; Ota et al., 2018), and specimens from all species collected were deposited in the fish collection of the Departamento de Zoologia e Botânica, Universidade Estadual Paulista “Julio de Mesquita Filho”, São José do Rio Preto (DZSJRP), São Paulo, Brazil (Tab. S1).

Limnological data. Water temperature was measured in situ using a multiparameter probe (HORIBA U53) and water transparency was determined by a Secchi disk. Water samples were collected to determine total nitrogen (N) (Mackereth et al., 1978) and total phosphorus (P) (Golterman et al., 1978). All measurements were determined in surface, middle and bottom depth. The quota data were obtained from the Reservoir Monitoring System available on the website of the National Water Agency (ANA, 2017). The reservoir water flow and rainfall data were obtained from the weather station at the Laboratory of Hydraulics and Irrigation of the Universidade Estadual Paulista (UNESP), Ilha Solteira, São Paulo, Brazil. The limnological characteristics of the fish farm and control in each season are shown in Tab. S1.
**Data analysis.** To verify the sufficiency of samples for ichthyofauna data, we generated rarefaction curves with interpolation and extrapolation (Chao *et al*., 2014) and 95% confidence intervals. To do that, we used species abundance data from the seasons within each area and individuals as the sampling unit.

To assess the effects of flooding on ichthyofauna attributes after the drought, we calculated total abundance, species richness, Shannon diversity index, and Pielou evenness (Magurran, 2004) for each collection in each sample area (collections were used as replicas of “season” (levels: drought and wet) and “area” (levels: control and fish farm). To compare each attribute between the seasons in each area and between the areas in each season, we tested the assumptions of normality and homoscedasticity through a graphical inspection of residuals and Levene’s test, respectively. Subsequently, we compared the groups (areas and seasons) using two-way ANOVA, and in case of observed differences between the groups, we applied the least-squares means for paired comparisons.

To calculate and compare β diversity between seasons in each area and between areas in each season, we used the PERMDISP analysis based on the Jaccard dissimilarity index using community presence/absence data. This method yielded a measure of overall total β-diversity (if based on presence/absence data) and community structural variation (if based on abundance data) (Anderson *et al*., 2006). Also, to test whether the ichthyofauna structure differs between seasons in each area, we applied one-way PERMANOVA based on Bray–Curtis dissimilarity (Anderson *et al*., 2006; Anderson, 2017), using a community abundance data matrix as dependent variable and area and season as independent variables. To unravel the reason for rejecting the null hypothesis of PERMANOVA (*i.e.*, location in the multivariate space or dispersion effects or both), the PERMDISP was then performed on the same Bray–Curtis matrix to test for differences in the multivariate dispersion (Anderson *et al*., 2006; Anderson, 2017). Because of the variation in the structure of the ichthyofauna, we applied the SIMPER overall pool analysis to verify the percentage of dissimilarity of fish communities and the species that most contributed to the differences (Clarke, Ainsworth, 1993). Furthermore, we applied a redundancy analysis (RDA) to verify the relationship of the species abundance data matrix with the limnological variables matrix. For this analysis, species abundance data were transformed by Hellinger distance, and ANOVA was performed to test the significance of each limnological variable for the entire model.

Statistical analyses were performed using the R software (R Development Core Team, 2019). Sample sufficiency analyses were performed with the aid of the “iNEXT” package and the iNEXT function (Hsieh *et al*., 2016). Species richness, Shannon index, and Pielou evenness were calculated by the “vegan” package using the diversity function (Oksanen *et al*., 2018). Two-way ANOVA, PERMDISP, one-way PERMANOVA, SIMPER, and RDA were performed with the aid of the “vegan” package, respectively using the aov, betadisper, adonis, simper, and RDA functions (Oksanen *et al*., 2018). The homoscedasticity of the models was verified by the “car” package using the leveneTest function (Fox, Weisberg, 2011). The paired comparisons of the models were performed with the “emmeans” package using the emmeans function (Lenth *et al*., 2018). The graphs were prepared using the emmeans function (Lenth *et al*., 2018) and the “ggplot2” package (Wickham *et al*., 2016). The level of statistical significance was set at $\alpha = 0.05$. 
RESULTS

We sampled 978 specimens in the control area (Drought: 473; Wet: 505), comprising a total of 25 species (Drought: 20; Wet: 21), and 1,452 in the fish farm area (Drought: 888; Wet: 564) with 24 species (Drought: 15; Wet: 24). Species accumulation curves show that sufficiency of samples was reached, following similar stabilization patterns in both seasons for the sample areas evaluated (Fig. S2).

Most species were shared between seasons and evaluated areas; however, there was variation in their abundance. *Schizodon intermedius* Garavello & Britski, 1990, *Heterotilapia buttikoferi* (Hubrecht, 1881), and *Megalancistrus paranus* (Peters, 1881) were exclusive to the control area, while *Hoplosternum littorale* (Hancock, 1828) and *Leporinus lacustris* Amaral Campos, 1945 were exclusive to the fish farm area. The non-native species *Geophagus sveni* Lucinda, Lucena & Assis, 2010 and *Plagioscion squamosissimus* (Heckel, 1840) were the most abundant in the drought and wet seasons in the fish farm area and the drought season in the control area, while *G. sveni* and *Serrasalmus maculatus* Kner, 1858 were the most abundant species in the wet season in the control area (Tab. 1).

Comparisons between the sampling seasons within each area (Fish farm: drought vs. wet; Control: drought vs. wet) showed no changes in total abundance (Fig. 3A); however, species richness was higher during the wet season in both areas (Control: $t = 3$, $p < 0.01$; Fish farm: $t = 2.24$, $p = 0.03$; Fig. 3B). The Shannon index and Pielou evenness were higher in the wet season only in the control area (Shannon: $t = 3.83$, $p < 0.01$; Pielou: $t = 2.14$, $p = 0.04$; Figs. 3C,D). Comparisons between areas within each season (Drought: fish farm vs. control; Wet: fish farm vs. control) showed differences only total abundance within drought season, with the higher value in fish farm ($t = 3.21$, $p < 0.01$; Fig. 3A).

The $\beta$ diversity differed between seasons only in the control area, it was higher values in the drought season (PERMDISP, $p = 0.03$; Fig. 4). The ichthyofauna structure also showed differences between seasons only for the control area (PERMANOVA, $R^2 = 0.31$; $F = 4.66$; $p = 0.03$) by a shift in the assemblage structure, and not by variation around the mean composition within groups (PERMDISP, $p > 0.05$), with a percentage of dissimilarity (SIMPER) of 62.29% and a high contribution of non-native and invasive species in the basin, *G. sveni* and *P. squamosissimus*, and only one native species (*S. maculatus*) (Tab. 2). In addition, for the control area, the “quota” variable was the only one that was significantly associated with the composition of the ichthyofauna (RDA-ANOVA; $F = 5.17$; $p < 0.01$), explaining 25.8% (adjusted $R^2$) of the variation in the dataset. The abundance of *P. squamosissimus* and *S. maculatus* were strongly influenced by the model and negatively and positively related to the increase in the quota, respectively (Fig. 5). The limnological variables did not have significant correlations with the composition of the ichthyofauna in the fish farm area.
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TABLE 1 | Taxonomic order of the sampled species and their abundance during the drought and wet seasons in the control area and fish farm area at the Ilha Solteira reservoir, Upper Paraná River, SP, Brazil. C = Characiformes, P = Perciformes, Ci = Cichliformes, and S = Siluriformes. Voucher specimens of DZSJRP.

| Species                                      | Order | Voucher | Abundance          |   |   |   |   |
|----------------------------------------------|-------|---------|--------------------|---|---|---|---|
| *Acestrorhynchus lacustris* (Lütken, 1875)   | C     | 21368   | 1                  | 1 | 2 | 7 |
| *Astronotus crassipinnis* (Heckel, 1840)     | Ci    | 21366   | 0                  | 0 | 2 | 1 |
| *Cichla kelberi* Kullander & Ferreira, 2006  | Ci    | 21360   | 1                  | 0 | 6 | 46|
| *Cichla piquiti* Kullander & Ferreira, 2006  | Ci    | 21361   | 0                  | 3 | 2 | 10|
| *Crenicichla britskii* Kullander, 1982       | Ci    | 21372   | 0                  | 3 | 1 | 4 |
| *Cyphocharax gillii* (Eigenmann & Kennedy, 1903) | C    | 21377   | 0                  | 0 | 2 | 1 |
| *Geophagus sveni* Lucinda, Lucena & Assis, 2010 | Ci  | 21365   | 371                | 165| 194| 156|
| *Heterotilapia buttiioferi* (Hubrecht, 1881) | Ci    | 21359   | 0                  | 0 | 0 | 2 |
| *Hoplias aff. malabaricus* (Bloch, 1794)     | C     | 21371   | 4                  | 11| 2 | 15|
| *Hoplosternum littorale* (Hancock, 1828)     | S     | 21356   | 0                  | 0 | 2 | 0 |
| *Leporinus lacustris* Amaral Campos, 1945     | C     | 21363   | 0                  | 0 | 1 | 0 |
| *Megalancistrus parananus* (Peters, 1881)    | S     | 21354   | 0                  | 1 | 0 | 0 |
| *Meynnis lippincottianus* (Cope, 1870)       | C     | 21358   | 30                 | 5 | 12| 35|
| *Oreochromis niloticus* (Linnaeus, 1758)     | Ci    | 21357   | 0                  | 2 | 5 | 0 |
| *Pimelodus platicirris* Borodin, 1927        | S     | 21316   | 162                | 10| 66| 4 |
| *Pinirampus pirinampu* (Spix & Agassiz, 1829) | S    | 21353   | 0                  | 1 | 2 | 0 |
| *Plagioscion squamosissimus* (Heckel, 1840)  | P     | 21369   | 241                | 196| 141| 53|
| *Pterygoplichthys ambrosettii* (Holmberg, 1893) | S   | 21355   | 6                  | 2 | 18| 8 |
| *Rhaphidodon vulgaris* Spix & Agassiz, 1829  | C     | 21317   | 11                 | 18| 8 | 12|
| *Roeboides descalvadensis* Fowler, 1932      | C     | 21367   | 11                 | 10| 5 | 2 |
| *Satanoperca pappaterra* (Heckel, 1840)     | Ci    | 21364   | 16                 | 4 | 7 | 15|
| *Schizodon intermedius* Garavello & Britski, 1990 | C   | 21362   | 0                  | 0 | 0 | 8 |
| *Schizodon nasutus* Kner, 1858               | C     | 21373   | 2                  | 3 | 38| 12|
| *Serrasalmus maculatus* Kner, 1858           | C     | 21374   | 8                  | 9 | 18| 91|
| *Serrasalmus marginatus* Valenciennes, 1837  | C     | 21376   | 11                 | 1 | 10| 2 |
| *Steindachnerina insculpta* (Fernández-Yépez, 1948) | C  | uncat.  | 13                 | 2 | 2 | 0 |
| *Triportheus nematuras* (Kner, 1858)        | C     | 21370   | 0                  | 26| 18| 21|
**FIGURE 3** | Box plots (minimum and maximum value = vertical line ends, standard error = box, and mean = horizontal line) of the ichthyofauna attributes in the control area and fish farm area, in the drought and wet seasons at the Ilha Solteira reservoir, Upper Paraná River, SP, Brazil. 

A. Total abundance; B. Species richness; C. Shannon index; D. Pielou evenness. Asterisks indicates significant upper value between seasons within each area. Hash indicates significant upper value between areas within each season.

**TABLE 2** | Contribution of species to the percentage of dissimilarity (SIMPER) of the ichthyofauna in the control area considering abundance data for the drought and wet seasons at the Ilha Solteira reservoir, Upper Paraná River, SP, Brazil.

| Species                  | Contribution (%) | Mean abundance |
|--------------------------|------------------|----------------|
|                          |                  | Drought        | Wet            |
| *Geophagus sveni*        | 24.84            | 27.5           | 26             |
| *Plagioscion squamosissimus* | 20.99          | 32.66          | 8.33           |
| *Serrasalmus maculatus* | 14.98            | 1.5            | 15.16          |
| Other (22 species)       | 39.19            | –              | –              |
DISCUSSION

Ichthyofauna responses to water level changes were different in the fish farm and control areas. Our results indicate that in the fish farm area, the change in water level did not influence the structure and composition of the ichthyofauna. Furthermore, in the control area, the wet season showed greater mean values of the species richness, Shannon diversity, evenness, and lower β diversity, and these results corroborating our hypothesis. Our analysis showed that the greatest difference observed in the structure of the ichthyofauna between the seasons in the control area is possibly associated with the variation in the quota. Such a pattern is also shown by other studies (Baumgartner et al., 2017, 2020; Lima et al., 2017), so we consider that the overall patterns and the possible explanations for spatial and seasonal variabilities described here will not change severely.

The greater mean values of the species richness in both areas during the wet season may be a result of the flooding of marginal areas, as observed in other studies (e.g., Agostinho et al., 2001, 2007; Fernandes et al., 2009). The flooding of these areas,
providing stable habitat and resources, such as greater availability of shelter and food, contributes to the increase in local species richness and diversity due to the attraction of species and population recovery (Lowe-Mcconnell, 1999; Bond et al., 2008). This increase in local diversity as a result of flooding in the control area is supported by higher mean values of the Shannon diversity and Pielou evenness. The increase in these indices indicates a decrease in the abundance of dominant species and a better quantitative distribution of rare species (Magurran, 2004). Conversely, the similarity in Shannon and Pielou indices between the seasons in the fish farm area can be explained by the tendency of dominance by a few species such as G. sveni and P. squamosissimus in areas close to fish farms. These species are non-native, generalist, and less susceptible to environmental variations (Moretto et al., 2008; Queiroz-Sousa et al., 2018).
Our results showed that the effect of flooding on the structure (PERMANOVA) and β diversity of the fish fauna in control area was not observed in the fish farm area. The continuous habitat structure provided by the enterprise in the arrangement of shelters (cages), feed, and attracted prey (e.g., invertebrates and small fish) is used directly by wild fish species (Pereira et al., 2019; Nobile et al., 2020), including the dominant species in our study (Kliemann et al., 2022). This reduces the seasonal effect of the availability of natural resources on the community (Nobile et al., 2018). Thus, the fish assemblage aggregates and persists in areas surrounding fish farms and tend to be dominated by non-native and generalist species (Daga et al., 2015; Pereira et al., 2019), contributing to greater biotic homogenization in fish farming areas.

Variation in assemblage structure is usually a response to the reordering of species abundance (Avolio et al., 2015). Hence, the change in the structure of the ichthyofauna between seasons in the control area may have occurred due to the increase in the abundance of some species due to the environmental conditions of the wet season. The presence of habitats for natural recolonization when the water level rises is one of the main factors for the recovery of native populations after drought impacts (Bond et al., 2008). The rise in water levels enables, for example, the intense growth of aquatic macrophytes (Gomes et al., 2012), which are used by specialist species as feeding habitat or a site for laying eggs on the roots and parental care of the offspring (e.g., S. maculatus) (Sazima, Zamprogno, 1985; Silveira Prudente et al., 2015). Thus, such interaction also contributes to explaining the increase in abundance and contribution of the native species S. maculatus by the SIMPER analysis in the control area, and its positive relation to the increase in the quota level.

The replacement of species in the control area showed susceptibility to water changes, which is strengthened by the variation in β diversity between the seasons in this area, a fact that was not observed in the fish farm area. In the control area, the decline in β diversity during the wet season was expected, given that β diversity in aquatic ecosystems is generally greater in drought periods (Thomaz et al., 2007). With the decrease of water levels, the progressive loss of the littoral zone and its associated vegetation can modify or to fragment habitats (Paller, 1997; Gomes et al., 2012), which may result in more dissimilar assemblages, showing a tendency towards an increase in β diversity (Anderson et al., 2011). Subsequently, with the prolonged rise in the water level and, as a consequence, more homogeneous habitats, the similarity between communities increases (Thomaz et al., 2007).

Contrary to our expectation, there were few differences in community structure between the control and fish farm areas in each season. The greatest abundance in the fish farm area was predicted as the effect of attraction and increased densities in areas surrounding fish farms (Barrett et al., 2019). This effect is mainly due to the increased abundance of opportunistic species around fish farms that contribute to differences between these areas and “natural” places (Nobile et al., 2018). Nevertheless, the similarity between the areas in the other ichthyofauna attributes is possibly related to the sharing of many non-native and generalist species, a common aspect in Neotropical reservoirs (Ortega et al., 2015; Queiroz-Sousa et al., 2018). Generalists dominate immediately after or during disturbances (Freitas et al., 2013), as many specialist species require medium-to long-term flooding to recover (Beesley et al., 2014), decreasing the spatial effect on diversity patterns expected between the fish farm and control areas.
We concluded that cage fish farming can interfere in ichthyofauna responses to water changes, with similarity in the structure traits and taxonomic compositional between the drought and wet seasons. The smallest change in the structure of the ichthyofauna in the aquaculture area (fish farm), even after extreme water changes, shows that this farming system contributes to the maintenance of non-native and dominant species such *G. sveni* and *P. squamosissimus*. Likewise, a good understanding of the quota regimes required for the conservation of native fish in regulated environments is essential and particularly useful for assemblage recovery after drought events, as recorded for the control area. We assess taxonomic aspects of the fish assemblages, and variations due to impacts of water regimes or fish farming may also occur on functional and genetic aspects. Thus, future studies on the effects of fish farming, focusing on drought and flooding periods, will be extremely relevant to the fields of aquaculture and ecology.

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**AUTHORS’ CONTRIBUTION**

Aymar Orlandi-Neto: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing-original draft, Writing-review and editing.

Rafael Vieira Amorim: Data curation, Formal analysis, Methodology.

Rosilene Luciana Delariva: Project administration, Supervision, Validation, Visualization, Writing-review and editing.

Antonio Fernando Monteiro Camargo: Funding acquisition, Methodology, Resources, Supervision, Validation, Visualization, Writing-review and editing.

Rosicleire Veríssimo-Silveira: Funding acquisition, Investigation, Project administration, Resources, Validation, Writing-review and editing.

Igor Paiva Ramos: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing-original draft, Writing-review and editing.

**ETHICAL STATEMENT**

SISBio authorization number 42229–1 and SisGen certificate A278D23. The collected specimens were euthanized (Ethics Committee on Animal Experimentation, authorization number 001/2014).

**COMPETING INTERESTS**

The authors declare no competing interests.

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