



A humped pattern of standing fish biomass in lowland subtropical streams as a response to a gradient of environmental degradation, species richness and season

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Received: 15 September 2022 / Revised: 2 May 2023 / Accepted: 6 May 2023 / Published online: 13 June 2023
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Abstract Human activities are one of the main causes of biodiversity loss and the reduction of ecosystem services. These activities, together with seasonality and the associated ecological and physico-chemical changes, are the main modulators of fish communities in subtropical streams. Using data from 62 streams from Uruguay, we analyzed the effect of environmental variables on several attributes of fish community structure. First, we evaluated the effect of climatic seasonality on fish biomass, density, mean body length and weight using a paired *t*-test. Secondly, we analyzed the relationship between seasonality, environmental variables (environmental degradation, watershed area, and habitat diversity), and species richness with fish biomass using a linear

mixed model. Fish biomass and density were higher in summer meanwhile, mean length was higher in winter. We found a humped relationship between biomass and environmental degradation in winter and summer, with low biomass in sites with high and low quality. Our model shows that species richness increase generates an increase in biomass, with the magnitude of this increase being greater during winter. In view of this results, we highlight that the humped pattern founded in our work should have special management attention to avoid misinterpretation of biomass increases caused by environmental degradation.

Keywords Fish community · Freshwater quality · Seasonality · Land use · Environmental degradation · Fish biomass

Handling editor: Sidinei M. Thomaz

Guest editors: Luiz Ubiratan Hepp, Frank Onderi Masese & Franco Teixeira de Mello / Stream Ecology and Environmental Gradients

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10750-023-05255-x>.

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Introduction

The change in land use caused by conversion of natural environments to croplands and urbanizations is one of the most critical global drivers of losses in biodiversity and ecosystem services (Millennium Ecosystem Assessment (MEA), 2005). Intensification of human land use in a river basin has a direct and indirect negative effect on the functioning of aquatic ecosystems (Allan et al., 1997; Ahearn et al., 2004; Moi & Teixeira de Mello, 2022). Different types of land use can deteriorate water quality due to the arrival of

nutrients, pesticides, heavy metals, hydrocarbons and drugs through runoff (Metzger et al., 2006; de Mello et al., 2018).

Nutrients reaching streams can have drastic effects on the nutrient load of the system, favoring eutrophication processes, organic matter accumulation, and decomposition rates (Turner, 2002; Dodds, 2006; Burwood et al., 2021). Eutrophication also affects ecosystem functioning, generating stoichiometric imbalances, altering the flow of energy and matter, and modifying oxygen availability. These changes, in turn, could affect the metabolism of the system (Kaelin et al., 2000; Wilcock & Nagels, 2001; Frost et al., 2002; Dodds, 2006; Barnes et al., 2014; Dodds & Smith, 2016).

Environmental degradation generated by land use could affect fish communities by decreasing both habitat diversity and species richness. The decrease in the number of different available habitats affects directly the community, as habitat diversity is positively related with the number of species, weakening interspecific interactions and promoting coexistence (Chesson, 2000; Harrison et al., 2005). Indeed, small species and juveniles could use a more significant number of refuges generated by habitat diversity, allowing the coexistence of predators and prey (Sih, 1992; Lusardi et al., 2018). As habitat diversity, richness is negatively affected by environmental degradation, where different effects caused mainly by urban and agricultural land use have been described in lowland streams. A loss of species and a decrease of the community mean body length, caused by an increase of the abundance of small tolerant species (i.e., *Cnesterodon decemmaculatus*) has been observed mainly in urban and agricultural streams (Chalar et al., 2013; Benejam et al., 2016; Barrios & Teixeira de Mello, 2022; Moi & Teixeira de Mello, 2022). Degradation effects could be attenuated or magnified depending on the climatic season. Increased temperature and reduced flow associated with summer could deteriorate water quality due to increased eutrophication processes and decreased dissolved oxygen (Van Vliet & Zwolsman, 2008; Klose et al., 2012).

All the above variables affect the ecosystem, altering human benefits or ecosystem services. Fish standing biomass can be considered an ecosystem service and a proxy of ecosystem functions. It refers to the total amount of living organisms -in this case fish- present in a given ecosystem. Biomass is considered

an ecosystem service for several reasons: as provisioning and cultural service in subsistence and sport fishing, as support service because it supports ecological functions such as nutrient cycling, predation, and maintaining biodiversity (Kitchell, 1979; Holmlund & Hammer, 1999; Hatton et al., 2015; Boerema et al., 2017; Moi & Teixeira de Mello, 2022; Pelicice et al., 2022). As a resource, fish biomass represents about 17% of all animal protein consumed worldwide by humans (FAO, 2020). In this sense, Uruguay stream fishes constitutes provisioning and cultural services, as subsistence fishing of medium-sized fish (as food) and small (for bait and aquariums) fishes; as cultural services due to recreational activities like sport fishing. However, these aspects have not been quantified in this region. As an ecosystem service, standing fish biomass is one of the most widely used metrics due to its relationship with ecosystem function since biomass could reflect secondary production (Cusson & Borget, 2005; Dolbeth et al., 2012). These services can be affected by the loss of species (e.g., Costanza et al., 2007; Moi & Teixeira de Mello, 2022), since a greater richness may also imply a more efficient use of the resources present in the ecosystem (“Niche complementarity”, Tilmann et al., 1997). Conversely, a reduction of species richness is related to a lower efficiency of biological communities affecting community functioning. In this sense, species loss is a negative factor that affects aquatic ecosystem services, such as standing biomass (Cardinale et al., 2012; MEA, 2005; Tilman et al., 2012; Moi & Teixeira de Mello, 2022).

In this work, we evaluated how natural variables (climatic seasonality and species richness) and human impacts generated by types of land use can affect fish standing biomass. For this purpose, we worked in small lowland streams along Uruguay in a gradient of environmental deterioration considering summer and winter. In this sense, we hypothesize that: (i) In the summer, streams will have higher fish density, biomass and richness because increased primary production during the warmer months allows the system to sustain this higher load. However, the increase in abundance will negatively impact community mean body length of fish community; (ii) Fish biomass will be lower at the extremes of the environmental degradation gradient, generating a humped pattern. In contrast to low-density livestock farming, agriculture and urbanization are associated with high nutrient

concentrations that favor primary producers generating a bottom-up effect on fish biomass by energy transference. Also, these types of land use are associated with lower oxygen concentrations; (iii) A positive relationship will exist between species richness and fish biomass. Therefore, sites with higher species richness will have higher biomass because species richness increases the efficiency in which resources are utilized.

Materials and methods

Study area

Uruguay belongs to the Neotropical biogeographic region, and most of the natural grassland has been transformed into cattle or crop areas (Cabrera & Willink, 1973). These activities occupy approximately 45% and 35% of the country's total land area. In addition, there is 15% occupied by afforestation, and 5% is occupied by urban areas (Hernández & Nuñez, 2015). Following Köppen's classification, Uruguay has a humid subtropical climate (Cfa), with

an average temperature ranging from 12 °C in winter to 25 °C in summer (Agudo, 1990).

Data were obtained from 62 streams of Strahler's order 2–4 belonging (average surface area of the basin = 14.9 Km², range = 1.2–68.4 Km², SD = 13.6) to three watersheds from Uruguay: Negro River (70,714 Km²), Santa Lucía River (13,433 km²), and Maldonado River (585 km²) (Fig. 1). Sampling sites were located in different micro basins, which allowed the independence in the values of land use variables between stream segments.

Land use variables

Watershed area was calculated using digital elevation models from the Alaska Satellite Facility (<https://search.asf.alaska.edu/#/?dataset=ALOS>) and the ALOS satellite from the Japan Aerospace Exploration Agency (JAXA). These models and land-use layers provided by the Uruguayan Ministry of Housing, Land Use Planning and the Environment (MVOTMA, <https://sit.mvotma.gub.uy/sit/>) were analyzed employing the free Geographic Information System QGIS (QGIS Development Team, 2018). A matrix was generated with information on the watershed area

Fig. 1 Uruguay location in South America (**a**; red square), map of Uruguay, and the 62 selected streams (**b**; red points). Example of streams with afforestation (**c**) and ranching cattle (**d**)



occupied by each land use type (urban, livestock, cropland, and forest) per site. In this case, the forest category includes only planted forests. Considering the watersheds studied, land use coverage ranged from zero for all uses to more than 98% for agriculture, livestock and forestry and 53% for urbanization (Table 1).

Environmental variables

Physical data (dissolved oxygen, conductivity, pH, and temperature) were obtained in situ with a multiparametric sonde YSI 6600 while fish samples were collected. Water samples were collected at each site for laboratory analysis of total nitrogen and total phosphorus (Koroleff, 1970; Valderrama, 1981). We used a modification of the NOVANA (National Monitoring and Assessment Programme for the Aquatic and Terrestrial Environments) methodology (Friberg et al., 2005; e.g., Teixeira de Mello et al., 2012, 2014; Borthagaray et al., 2020) for stream habitat

characterization. A stream section of fifty-meter in length was determined, marking six perpendicular transects at 0, 10, 20, 30, 40, and 50 m. In each transect, depth measurements were taken in addition to a qualitative evaluation of the substrate (percentage of sand, mud, clay, gravel, and stone) and vegetation cover every 25 cm. We generated the variable habitat diversity by applying Shannon's diversity index with substrate and vegetation cover data (Table 2).

Fish community

Fish were collected in 62 streams by point electrofishing (P) in summer and winter between 2007 and 2019 by performing 50 electric pulses on 50 m of the stream with an electrofisher powered by a 230 V generator (following Teixeira de Mello et al., 2014). In this way, fish communities were sampled once in winter and again in the following summer. In each electric pulse, all fishes were captured using hand nets (40 cm diameter, 0.2 cm mesh), and euthanized using

Table 1 Mean, standard deviation (Std), and the maximum area occupied by each land use in all the stream watersheds are presented as a proportion of the total area (Relative) and area as squared kilometers

Land use	Relative			Area (Km ²)		
	Mean	Std	Max	Mean	Std	Max
Urban	0.06	0.14	0.53	0.73	2.56	12.25
Agriculture	0.33	0.32	0.99	5.33	9.07	43.73
Cattle	0.48	0.29	0.99	6.18	7.28	49.01
Afforestation	0.14	0.28	0.98	1.99	5.19	35.12

Table 2 Mean, range and standard deviation (Std) during summer and winter of the environmental variables analyzed

Variable	Summer			Winter		
	Mean	Range	Std	Mean	Range	Std
Total phosphorus (µg/l)	338.57	6.31–3091.83	585.23	292.70	7.93–1424.28	357.43
Total nitrogen (µg/l)	1400.83	67.87–9795.00	1825.20	1474.86	78.37–9308.35	2074.85
O ₂ (mg/l)	6.80	2.28–14.28	2.46	8.32	2.02–13.19	2.80
Conductivity (µS/cm)	428.34	56.34–1057.00	281.04	442.54	30.00–1192.40	288.78
Temperature (°C)	21.31	16.08–28.12	2.56	13.53	7.47–22.83	1.47
Width (m)	3.39	1.25–7.54	1.46	3.56	1.20–9.19	1.66
Depth (m)	0.25	0.10–0.73	0.17	0.33	0.13–0.67	0.21
Sand (%)	25.36	0.00–95.5	22.75	28.45	0.00–95.50	24.68
Gravel (%)	17.17	0.00–75.00	21.59	16.47	0.00–75.00	22.22
Stone (%)	30.97	0.00–95.00	30.11	26.52	0.00–99.00	28.57
Clay (%)	8.82	0.00–100.00	17.45	8.78	0.00–69.75	17.98
Mud (%)	18.33	0.00–100.00	25.47	19.58	0.00–93.50	27.27
Vegetal cover (%)	22.31	0.00–81.96	19.05	22.46	0.00–86.00	20.30

2-phenoxyethanol (CHEA protocol No 603, 101). In the laboratory, all sampled fishes were identified to species level, counted, and measured (standard length at 0.1 cm; weight at 0.01 g). Since multiple pass electrofishing (MP) is the only method that allows an estimation of biomass (BM) and abundance by area, we used the abundance relationship between MP and P observed by Teixeira de Mello et al. (2014) using the equation:

$$\log(Y) = 0.98 \log(X) + 0.39$$

were Y is the number of individuals collected by multiple pass electrofishing and X is the number of individuals collected by point electrofishing. Using the corrected number of individuals and the area of each fished stream segment (data obtained from the ANOVA) we could calculate fish density (individuals/m²). Multiplying density by the average weight of each individual (g/individual) we obtained average biomass per square meter (g/m²). Finally, richness was calculated as the number of species by rarefaction to remove the effect of the number of individuals (Hsieh et al., 2020).

Statistical approach

Seasonal differences between fish community metrics (density, species richness, biomass, mean length, and mean weight) were evaluated using a paired t -test. In order to evaluate if the seasonal differences in biomass, density and mean standard length was caused by a particular species this variables were analyzed for those species that represent 90% of the total biomass. For this purpose, a paired t -test was carried out for each species biomass, density and mean body length between seasons.

To generate a new variable that reflects the environmental degradation, a principal components analysis (PCA) was performed after standardizing and centering environmental variables (total phosphorus and nitrogen, dissolved oxygen and conductivity) and types of land use (urban, afforestation, cattle and agriculture) with a covariance matrix. The number of statistically significant components was estimated using the “broken stick” method included in the “PCDimension” package (Coombes & Wang, 2019). The broken stick method showed that the first principal component (PC1) was the only significant.

A linear mixed model was built to evaluate the possible effect of environmental degradation, species richness, watershed area, habitat diversity, and season over fish biomass. Before modeling, the possible distribution of the fish biomass per square meter (BM) was evaluated using the “fitdistrplus” package to select the family of the LMM (Delignette-Muller & Dutang, 2015). Two distributions (Normal and lognormal) were fitted and Akaike’s criterion (AIC) was used to determine the best fitting. This analysis showed that BM was best suited to a lognormal distribution. Then, simple linear regressions were made between the response variable (BM) and the explanatory variables (PC1, richness, watershed area, and habitat diversity) as an exploratory of the relationship (linear or nonlinear) between variables. This relationship was evaluated by observing the tendency line in a visual exploration (Online Appendix S1: Fig. S1). This exploration shows that PC1 has a quadratic relationship with fish biomass, indicating that it should be appropriate to include a quadratic term of this variable in the model. Using all the data mentioned above, a first linear mixed model was generated with the “lme” package (Pinheiro et al., 2020). In this way, PC1, PC1², richness, habitat diversity, watershed area, and season were established as fixed effects and stream identity as a random effect. Stream identity was used as a random effect to remove the variation generated at each site by its individual life history. The model selection consisted of generating simpler models in which variables that do not contribute significance are removed. This simplified model was then compared with the previous one using the likelihood ratio test (LRT). If the LRT did not detect significant differences between the models, they are equivalent, so the selection continued with the simpler one. A final model that did not include habitat diversity or watershed area was produced with these criteria. Using the “DHARMA” package, model residuals were simulated to evaluate normality and variance homogeneity (Harting, 2020). The residual analysis confirmed that the model meets the assumptions of normality and variance homogeneity. The final model was adjusted and presented using the “ggeffects” package (Lüdtke, 2018). This package allowed us to generate a graphical visualization of the adjusted model’s predictions. All statistical analyses were performed with free software R (R Core Team, 2020).

Results

We caught 49,334 individuals belonging to 63 species, six orders, and 15 families, with Characiformes being the most abundant order with 22 species. The species with the highest abundance was *Cnesterodon decemmaculatus* (Jenyns, 1942) (Cyprinodontiformes, Poeciliidae) with 29,955 individuals. This species, in conjunction with *Cheirodon interruptus* (Jenyns, 1942) (Characiformes, Characidae) was the most frequent, being present in 58 streams. In terms of biomass of all streams, *Gymnogeophagus terra-purpura* Loureiro, Zarucki, Malabarba & González-Bergonzoni, 2016 (Cichliformes, Cichlidae) was the species with the highest biomass per square meter, followed by *Hoplias argentinensis* (Rosso, González-Castro, Bogan, Cardoso, Mabragaña, Delpiani, Díaz de Astarloa, 2018) (Characiformes, Erythrinidae). Given their high abundance, *C. decemmaculatus* ranked fourth among the species with the highest biomass despite being a small size species (1–2 cm approx.).

Regarding community attributes, biomass and number of individuals per square meter were higher in summer, the mean body size was larger in winter and there was no difference in species richness and mean body weight between seasons (Table 3). The analysis by species shows that biomass was significantly higher in winter for *Psalidodon eigenmanniorum* (Cope, 1894) (Characiformes, Characidae), *Oligosarcus jenynsii* (Günther, 1864) (Characiformes, Characidae) and *Cyphocharax voga* (Hensel, 1870) (Characiformes, Curimatidae). In terms of density, *C. decemmaculatus* showed significantly higher densities in winter. In terms of mean length, *C. decemmaculatus* and *Hyphessobrycon meridionalis* Ringuelet, Miquelarena & Menni, 1978 (Characiformes, Characidae), showed significantly greater lengths in winter. In addition, there was a tendency for most species

to show a higher biomass and density in summer with a smaller body size than in winter (Fig. 2).

The first component of the principal components analysis explained 45.6% of the variance and resumed the changes in water quality between cattle and afforested watersheds by one hand, and urban and agricultural by the other hand. Cattle and afforestation watersheds were mainly associated with high oxygen concentrations, low nutrient concentrations, and low conductivity. In contrast, urbanization watersheds showed high nutrient concentration and conductivity, with low dissolved oxygen. Finally, mainly agricultural watersheds showed intermediate levels of nutrients, conductivity, and oxygen (Fig. 3). It is important to highlight that in several streams, phosphorus and dissolved oxygen levels exceeded the limits established by Uruguayan government (maximum of 25 µg per liter for phosphorus and minimum of 5 mg per liter for oxygen) (Table 2). The correlation of each variable with component 1 is shown in Table 4.

After the model selection process, the final linear mixed model showed that only PC1 (and its squared variant), species richness, and season had significantly influenced fish biomass per square meter (BM) (Table 5). In addition, there was a significant interaction between richness and seasonality. Considering the random effects, the model explained 55% of the variance (conditional $R^2=0.55$). Finally, the model could be summarized in the following equation:

$$\log(\text{BM}) = 0.12 \text{PC1} - 0.09 \text{PC1}^2 + (0.45 - 0.27x)\text{Richness} + (1.9 + 0.42x)$$

with x taking values of 0 in summer and 1 in winter.

The linear mixed model revealed that BM has a hump-shaped response to environmental degradation. The lowest BM was observed in streams with low and high environmental degradation levels, associated with watersheds whose main land

Table 3 Mean, standard deviation (Std), minimum and maximum of the fish community characteristics in winter and summer

Results of the two-sample paired t -test for each community feature between seasons (t -statistic and P -value)

Feature	Summer				Winter				t	P value
	Mean	Std	Min	Max	Mean	Std	Min	Max		
Biomass (g/m ²)	15.10	25.84	0.27	102.32	7.61	7.36	0.29	37.17	2.63	0.01
Estimated richness	18	8	3	45	18	8	3	51	-0.26	0.79
Density (ind/m ²)	9.68	58.10	0.17	157.08	4.01	6.08	0.06	46.58	2.82	0.01
Mean weight (g/ind)	3.51	0.79	0.18	49.23	3.04	0.26	0.36	11.63	-0.55	0.58
Mean length (cm/ind)	3.65	1.36	1.66	8.47	3.98	1.23	2.10	7.61	2.39	0.02

Fig. 2 Mean differences between Winter (left) and Summer (right) in mean biomass per square meter (a), mean density (b), and mean standard length for fish species that represent the 90% of total biomass collected. Means between seasons were evaluated with paired *t*-test and differences are pointed out with an asterisk. *0.005; **0.001; ***0.0001. Note that the density value for *Cnesterodon decemmaculatus* should be multiplied by a factor of ten

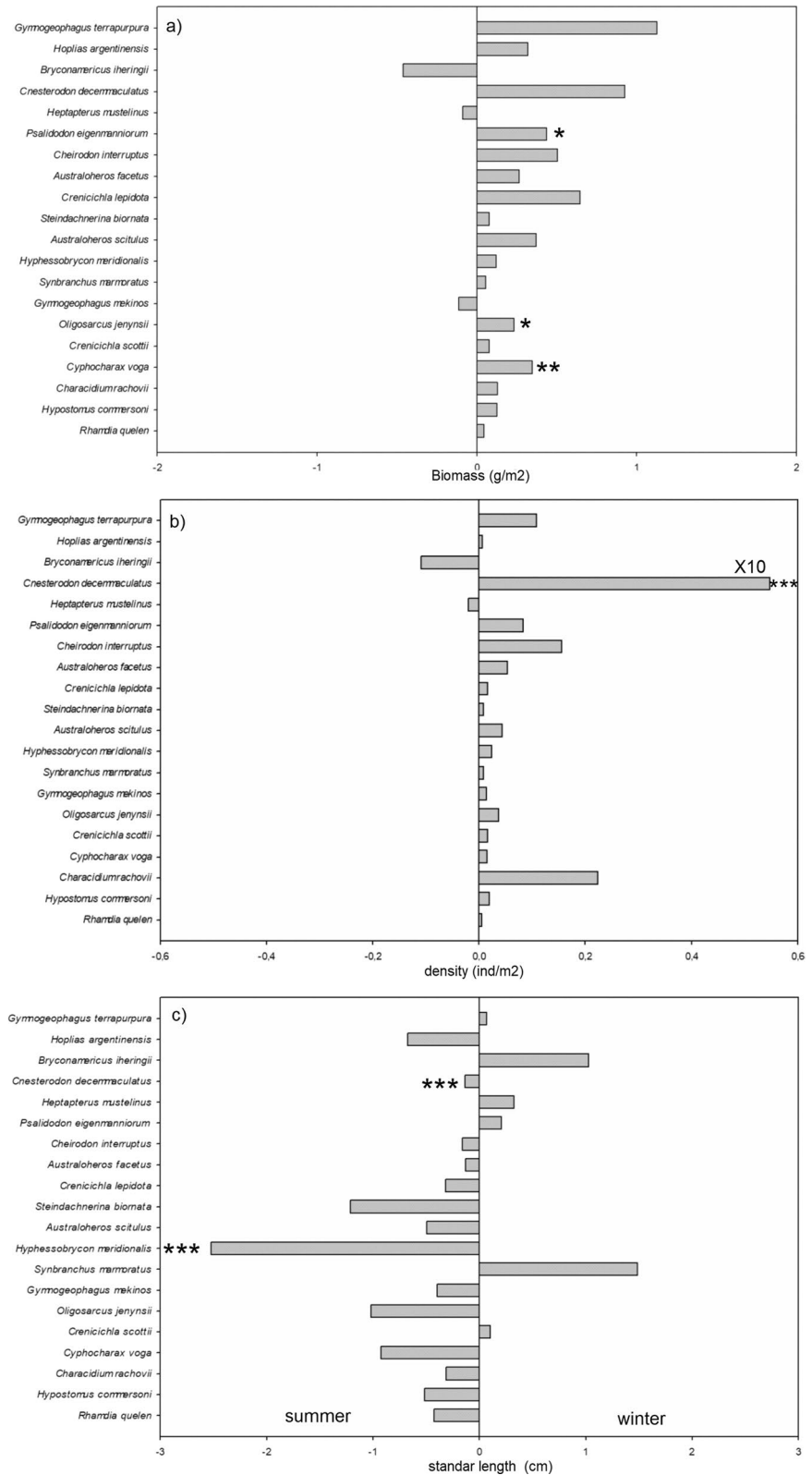
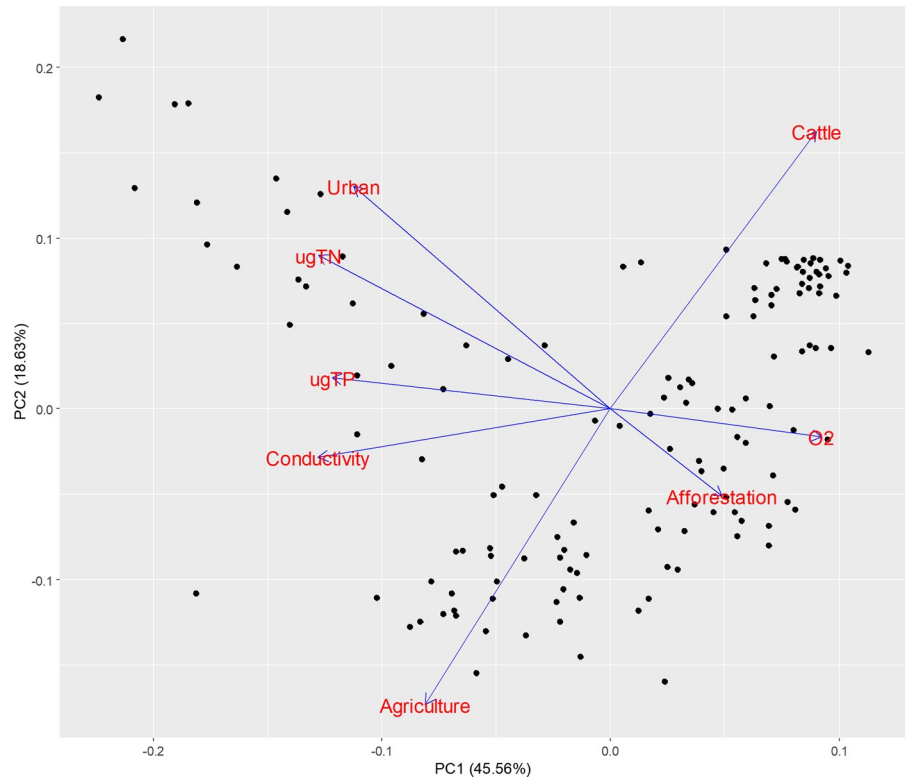


Fig. 3 Graphical result of the Principal Components analysis showing the streams ordination (black dots) in the function of the analyzed variables: types of land use (Urban, Agriculture, Cattle, and Forestry), total phosphorus (TP), total nitrogen, conductivity, and dissolved oxygen (O₂)



use was cattle-afforestation and urban, respectively. Meanwhile, the highest levels of BM were detected at medium degradation levels related to mainly agricultural watersheds (Fig. 4). Moreover, there was a seasonal effect since BM was significantly higher in summer.

In terms of species richness, there was a positive relationship between the number of fish species and BM. Seasonality also influenced this relationship; the slope was less steep in winter than in summer. When the trophic groups were analyzed separately (Carnivore, Omnivore and Detritivore), we found that the increase in the number of species generated an increase in biomass in each trophic group except in detritivores, where the slope was not significant (Online Appendix S1: Methods, Fig S2, Table S1).

Discussion

Land use and water quality

Environmental and land use data summarized with the PCA resume the patterns of environmental

variation in relation to land use and nutrient concentrations among the studied environments. The relationship between PC1 and land use fits with results from other works, detailed that land use in the watershed affects the water quality (Bolstad & Swank, 1997; Tong & Chen, 2002; Goyenola et al., 2020). Our results show that afforestation and low density ranching were principally associated with better water quality metrics than urban and agriculture. As reported in the bibliography, afforestation was associated with lower degradation because it reduces soil erosion and nutrient runoff from the watershed (van Dijk & Keenan, 2007). Although intensive cattle ranching generally has a negative impact on water quality, it is reported that in zones with low livestock density, the impact of this type of land use on water quality is minor (de Mello et al., 2018). This could happen in the studied streams because all the studied cattle watersheds were occupied by low density ranching. Agriculture and urbanization show to be the types of land use with the more significant impact on water quality, biotic integrity indexes, and ecosystem services (Wang, 2001; Benejam et al., 2016; Alvareda et al., 2020; Goyenola et al., 2020; Alcantara et al.,

Table 4 Loadings of the analyzed variables and principal components 1

Variable	PC1
Urban	-0.38
Agriculture	-0.27
Cattle	0.23
Afforestation	0.18
TP ($\mu\text{g/l}$)	-0.45
TN ($\mu\text{g/l}$)	-0.42
Conductivity ($\mu\text{S/cm}$)	-0.44
O ₂ (mg/l)	0.36

2021; Moi & Teixeira de Mello, 2022). Phosphorus and nitrogen concentrations and organic matter in water increase in agricultural and urban watersheds (Lenat & Crawford, 1994; Paul & Meyer, 2001; Silva et al., 2011; Beckert et al., 2011). Larger quantities of organic matter increase metabolism associated with

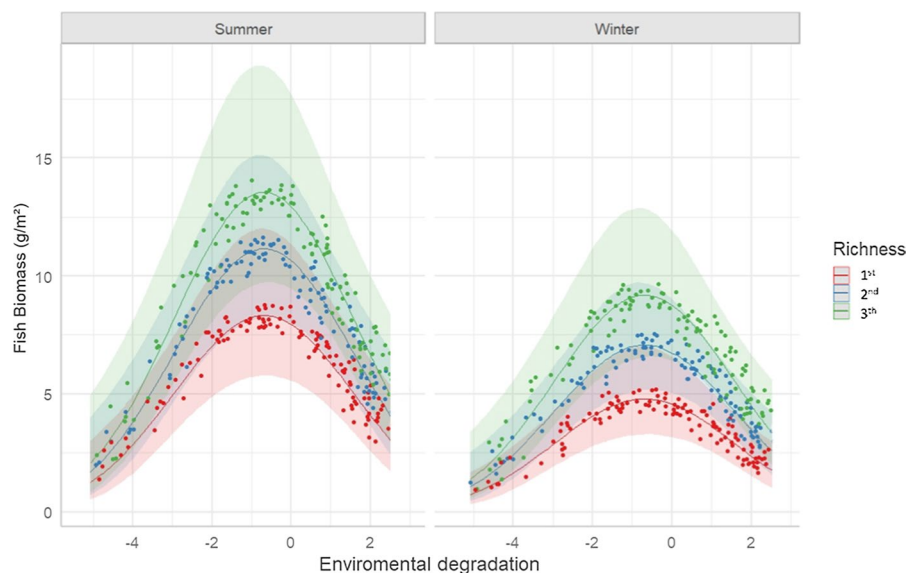
higher decomposition rates and oxygen demand. This process causes oxygen depletion in agricultural and urban streams, as observed in our data (PCA) (Miskewitz & Uchrin, 2013). In this sense, 25% of the studied streams in summer presented high nutrient values (total phosphorus mean = $428.9 \pm 81.5 \mu\text{g/l}$; total nitrogen mean = $2191.1 \pm 505.9 \mu\text{g/l}$) and low oxygen concentrations (mean = $3.6 \pm 0.2 \text{ mg/l}$), indicating eutrophication processes (Dodds et al., 1998) and harmful conditions for fishes (i.e., concentrations lower than 5 mg/l ; Franklin, 2014) as recognized in the Uruguayan legislation (class 1 to 3; National Decree, Dec, 2019, 253/79, MVOTMA of the Water Act Law No. 14.859/78).

Fish community characteristics

Species richness found in the analyzed streams was similar to that reported for similar systems but lower impacted from Uruguay, Argentina and Brasil (see

Table 5 Linear mixed model coefficients (Coef.), confidence interval (CI), standard deviation (Std), *t* statistic, and *P*-value

Fixed effect	Coef	CI	Std	<i>t</i>	<i>P</i> value
PC1	-0.12	(-0.25 to 0.02)	0.07	-1.74	0.08
PC1 ²	-0.09	(-0.14 to (-0.04))	0.03	-3.77	<0.005
Winter richness	0.45	(0.21–0.70)	0.13	3.62	<0.005
Summer richness	0.18	(-0.57 to 0.03)	0.15	-1.77	0.08
Winter	1.90	(1.60–2.20)	0.15	12.5	<0.005
Summer	2.32	(2.03–2.61)	0.15	15.60	<0.005

Fig. 4 Relationship between fish biomass per square meter (g/m^2) and environmental degradation, species richness in summer and winter. Environmental degradation in the x-axis goes from high (left) to low (right) degradation. Different colors indicate richness percentile: first quartile (red), second quartile (blue), and third quartile (green). The points correspond to model predictions obtained with the package “ggeffects”

revision on Teixeira de Mello et al., 2012). This could indicate that our sites are representative of the region in terms of richness. However, the maximum densities and biomass found in this study (157 ind/m² and 102 g/m², respectively) are much higher than those reported in other regional studies (21 ind/m² and 30.7 g/m², respectively—Teixeira de Mello et al., 2012). These differences may be because in this work, we include systems with a medium impact that increase the fish densities and biomass. In watersheds with a medium to high impact (principally agricultural and urban streams), the size spectrum is wider than in non-impacted systems (Benejam et al., 2016). This may be due to an increase in the number of small species associated with the increased impact of land use (Pott et al., 2021). The increase in small species abundance associated with these watersheds could be generating an increase in the density. In our case, the sites with higher densities were associated with agricultural watersheds, were tolerant and small-sized species like *Cnesterodon decemmaculatus* were dominant.

Seasonal effects on the fish community

As reported previously for streams in the same region, individual density at community level was greater in summer than in winter (González-Bergonzoni et al., 2016), also in summer, a higher biomass and a smaller body size of fish were observed (Table 3). One possible mechanism to explain the difference found, lies in fish reproductive periods. Temperature is critical for fish reproduction and reproductive activity is generally concentrated in warmer months (Andrade & Braga, 2005). Although our results shows that significant differences at the species level occur only in a few cases, such differences generate differences at the community level. This may be a result of spring breeding events, in coincidence with previous observations (e.g., *Bryconamericus iheringii*, González-Bergonzoni et al., 2016). In our case, it is worth noting the significant increase in the density of smaller individuals of *Cnesterodon decemmaculatus*, which increased from 1.6 to 7.1 ind/m², which, being a small, non-migratory species, makes the reproduction peak evident.

A larger number of juveniles could be affecting not only densities but also the mean body length of the community. Furthermore, the observed data

could be explained by the temperature itself. The increase in density associated with a decrease in size is in line with what is proposed in the metabolic theory of ecology (MTE) since smaller individuals would be most expensive in terms of energy than larger ones, then they are expected to be more abundant during periods of higher temperature (Brown et al., 2004).

The increase in fish biomass/m² in summer may be due to reproductive events or the arrival of individuals from other locations. However, it is important to consider how the system could maintain this higher biomass. In this way, primary production is essential in sustaining the food web's upper levels controlling upper biomass levels through a bottom-up mechanism (Downing et al., 1990; Rosemond et al., 1993; Borer et al., 2006). An increase in light availability (and temperature) during the summer, stimulates primary productivity, increasing standing biomass of consumers (Kevern & Ball, 1965; Rosemond et al., 2000; Dejen et al., 2017).

Fish biomass and environmental degradation

The results found for fish biomass show a similar behavior to that proposed for richness in the intermediate disturbance theory (Connell, 1978). As observed in our results, fish biomass use to increase with increased richness. Therefore, in intermediate degradation (disturbance) scenarios, richness and thus biomass would be higher than in less and high degradation extremes. Fish biomass is lower at high nutrient levels and low oxygen concentration sites. These conditions could be considered an intense stress generated by the high level of environmental degradation, where only a few species considered tolerant can survive (Wang et al., 1997; Morgan & Cushman, 2005). Our results showed that *C. decemmaculatus*, a small and tolerant omnivore, is the dominant species in the most deteriorated streams, as previously reported (Benejam et al., 2016). This biomass pattern was also observed at low environmental degradation sites. Low nutrient concentrations associated with these environments could affect primary productivity (e.g., filamentous algae, Gudmundsdottir, 2011), limiting the growth of high trophic levels, which harms the total standing biomass (Malzahn et al., 2007; Moi & Teixeira de Mello, 2022).

Fish biomass and species richness

Biomass increase associated with increased species richness is a pattern already reported in the literature (Borthagaray et al., 2020; Woods et al., 2020). A higher species number could favor an optimal use of the resources available in the aquatic systems (Hargrave, 2009). This efficiency is related to a biomass increase in each functional group, where abundant and dominant species determine how resources are exploited (Bellwood et al., 2003; Cardinale et al., 2012). In our case, the final model shows that adding one species has differential effects depending on the season. Therefore, an increase in fish species richness is accompanied by an increase in fish biomass in omnivores and carnivores, the slope of this increase is greater in winter. Considering that there are no significant differences in richness between seasons, the observed pattern may be due to species identity or the traits of the added species. In addition to species identity, trophic role (Moi & Teixeira de Mello, 2022) and interspecific interactions could be affecting the ecosystem function (biomass production) (Kirwan et al., 2009). This may indicate that, in terms of biomass increase, it is important not only to know how many species are being added, but also their trophic groups. Although biomass tends to grow with richness, the trophic group to which the new species belongs may affect the magnitude of this growth (e.g., in this work omnivores *versus* detritivores). These results show the relevance of knowing how different traits (e.g., trophic group, spawning season) can affect biomass production in subtropical streams.

Conclusion

Our findings highlight the importance of climatic seasons in modulating fish biomass changes caused by land use. It is important to highlight the humped response pattern found because, like other environmental responses to impacts, biomass response was non linear. This response requires special management attention because initially an increase in deterioration shows increased biomass. This pattern could be seen as positive until the deterioration continues and the effects can be irreversible as the community may collapse (known as a tipping point). It is important to continue generating information about the fish

community's responses since they are strong indicators of environmental degradation and provide countless services for human well-being (Pelicice et al., 2022).

Acknowledgements We would like to thank Guillermo Goyenola, Camila Vidal, Martin Pacheco, Lucia Hurtado, Nicolas Vidal, Clementina Calvo, and Maite Burwood for helping with sampling campaigns. We also thank Claudia Fosalba for nutrient analysis and German Taveira for his help with the geographic information analysis. Intendencia Municipal de Canelones supported the sampling campaign in the streams from the locality of Canelones. FTM was supported by ANII National System of Researchers (SNI) and PEDECIBA-Geociencias and Biología.

Author contributions GT: Conceptualization, Formal analysis, Investigation, Data Curation, Writing—Original Draft, Project administration. FTdM: Conceptualization, Methodology, Investigation, Resources, Data Curation, Writing—Review and Editing, Supervision, Project administration.

Data availability The datasets generated and analyzed during the current study will be made available from the corresponding author upon reasonable request.

Declarations

Conflict of interest The authors declare no conflicts of interest.

Consent to participate All authors consent to participate in this research.

Consent for publication All authors consent to publish this research.

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