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RESEARCH ARTICLE

Hydrologic variability effects on catches of *Prochilodus nigricans* in the lower Amazon

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Abstract

Flooding events in large rivers, termed flood pulses, expand and contract habitat available for fish populations, affecting fish abundance and catches. Here, we investigated if river hydrologic variability affected catch of curimatã (*Prochilodus nigricans*), a widely distributed and economically important fish species of the Amazon Basin. Using fish catch and fishing effort data for the lower Amazon region collected between 1993 and 2004, we performed an (i) analysis of covariance (ANCOVA) to understand the intra-annual relationship, and (ii) a cross-correlation function (CCF) to assess the inter-annual lag associated between river water levels and catches. We found that the intra-annual relationship between monthly river water levels and monthly catches of *P. nigricans* was negative, resulting in greater catches during lower river water levels and vice versa. We also found positive correlations with an inter-annual lag of 15-months between river water levels and catch, indicating that years with more extensive flooding lead to greater than normal catches of *P. nigricans* 15 months later. Increased flooding can be hypothesized to lead to increased survival and growth rates of *P. nigricans*. This dependency of catches of *P. nigricans* on river hydrological cycles underscores the threat posed by ongoing hydrological alterations to fish-related food and income security in the region. Further research is necessary to assess the extent to which such hydrological effects can impact multispecies fisheries catches in light of growing levels of fishing pressure.

Keywords Fish · Floodplain · Flood pulses · Temporal variations · Brazil

Introduction

The hydrology of large rivers controls the population dynamics of many aquatic species, including the amount of fish biomass available in the system (Welcomme 1985). Seasonal and predictable flooding events in large rivers, termed flood pulses, expand and contract habitat available for fish populations, thereby dictating ecological conditions for fishes to complete their life cycles (Junk et al. 1989). However, the hydrology of most rivers worldwide is increasingly disrupted by human activities such as climate change (Freitas et al. 2013; Barros and Albernaz 2014), construction of dams (Freitas et al. 2013; Begossi et al. 2019), and land cover changes (Castello et al. 2019a; Barros et al. 2020). There is therefore a need to improve understanding of the impacts of such hydrological alterations on fish populations and particularly their fish catches, which underpin many valuable ecosystem services worldwide (Welcomme et al. 2010).

Fish biomass available for harvesting has been shown to depend on the length and duration of the flood cycle (Bayley 1995; Fabré et al. 2017). For most species, river floods are associated with growth and reproduction while river low water seasons are associated with increased natural and fishing mortality. Generally, rising river water levels prompt

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fish to spawn and migrate onto flooding floodplain habitats, where fish of all ages find protection from predators and abundant plant-based food resources, including algae, detritus, and tree fruits and seeds (Fernandes 1997; Agostinho et al. 2004; Castello et al. 2019b). The decline of water levels prompt fish to migrate back to river channels and floodplain lakes, where they face increased densities, high fishing and predation rates, and poor water quality (Lagler et al. 1971; Junk 1985). Variability in river hydrology in any given month or year can thus affect fish catches. This can occur as water levels affect fish catchability, or higher-than-normal production or mortality processes in a given year can lead to more or less fish biomass for harvesting in subsequent years when the fish grow large enough to be captured (Halls and Welcomme 2004).

In the Amazon Basin, which for the most part still possesses a relatively intact river hydrology (Castello and Macedo 2016), the effects of hydrologic variability on fish biomass and catch have been studied at different levels of species groupings, including all species together (i.e., multispecies; Mérona and Gascuel 1993; Castello et al. 2015), trophic groups (Castello et al. 2015), longevity (Isaac et al. 2016; Fabré et al. 2017), and also separately for two species *Colossoma macropomum* (Castello et al. 2019b) and *Prochilodus nigricans* (Bayley et al. 2018). Of the latter two species, *P. nigricans* is a relatively well-studied species that has a very broad geographical distribution and sustains some of the largest fish catches in the Amazon (Mota and Ruffino 1997; Castro and Vari 2004; Soares et al. 2008; Anderson et al. 2009; Silva and Stewart 2017).

Prochilodus nigricans encompasses a homogeneous population along the Amazon River main channel (Machado et al. 2017); it is a detritivore that plays a key role in the transfer of energy from basal resources to higher levels of the food web, thus increasing the ecological efficiency of fish production (Winemiller and Jepsen 1998; Taylor et al. 2006; Anderson et al. 2009). *Prochilodus nigricans* migrate out of floodplain lakes during rising water levels to spawn in the open waters of the main river channel, and then migrate laterally to the vegetated habitats of the floodplain (Araújo-Lima and Ruffino 2003; Silva and Stewart 2017). The larvae migrate downstream for up to 15 days as they are carried into the flooded areas where they find abundant food and shelter (Araújo-Lima and Oliveira 1998). The dependence of *P. nigricans* on the flood pulse appears to be a key mechanism through which hydrological variability affects the dynamics of its population. Santana and Freitas (2013) performed a time series analysis and found that catches of *P. nigricans* followed either a 2–3-month cycle or a yearly cycle in which higher-than-normal catches in a given month or year tended to remain higher-than-normal for 2–3 months or years. They speculated that such periodicity was due to variability in river water levels affecting the amount of time available for their young to inhabit the flooded floodplains. Bayley et al. (2018) developed an empirical model of the population dynamics of *P. nigricans* and assessed the extent to which the annual amount of the moving littoral of the floodplain in any given year predicted an age cohort's abundance and catch in subsequent years. They found that the extent of flooding of the moving littoral was positively related to the abundance of age two cohort. But, contrary to expectations, they did not find that extent of flooding of moving littoral affected catch, probably because of their small sample size (n = 14-years of data) and mixing of age classes in the catch.

Within this context, this study sought to assess whether hydrological variability does affect catches of *P. nigricans.* Because this species is relatively short-lived, its catches possess a small number of age classes, making possible hydrological effects to be more easily detectable than in long-lived species such as *C. macropomum*. This study aimed to improve understanding of how hydrological variability affects catches of *P. nigricans*. We addressed two interrelated research questions at two temporal scales of analysis. First, we sought to understand the intra-annual relationship between monthly river water levels and monthly catches of *P. nigricans*. Then, we assessed the inter-annual lag associated between monthly river water levels and monthly catches of *P. nigricans*. The rationale was first understanding how seasonal flooding affected catches of *P. nigricans*. Then, building on this, understanding how interannual variability in seasonal flooding affected catches of *P. nigricans* through inferred effects of flooding on their population dynamics. The results of our analysis can inform environmental assessment and management processes by specifying the ways through which fish populations and catches may be disrupted, as land cover changes, hydropower dams, and other forms of hydrological alteration continue to modify river flows globally.

Methods

Study area

We conducted our study in whitewater 'várzea' floodplains of the lower Amazon River in Brazil (Fig. 1). In 2019, the region had 237,284 inhabitants (IBGE 2019) with most people living in urban or rural communities by riverbanks and floodplain lakes. The amplitude of the annual variation of the Amazon River water level in our study area is six meters, with the maximum seasonal water level in May and the minimum in November. The floodplains are flooded by nutrient-rich waters stemming from the Andes Mountains, forming a complex mosaic of plant communities (herbaceous, aquatic macrophytes, shrubs, and forests), lakes, and channels (Junk and Piedade 1997; Hess et al. 2003). Several

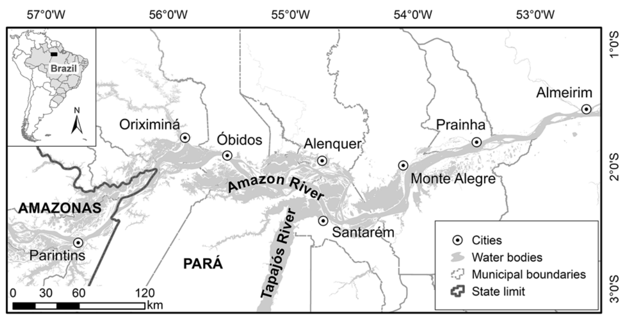

Fig. 1 Location of the study area and headquarters of the municipalities where fishing landing data were collected along the Amazon River, located along the limits between the states of Amazonas and Pará

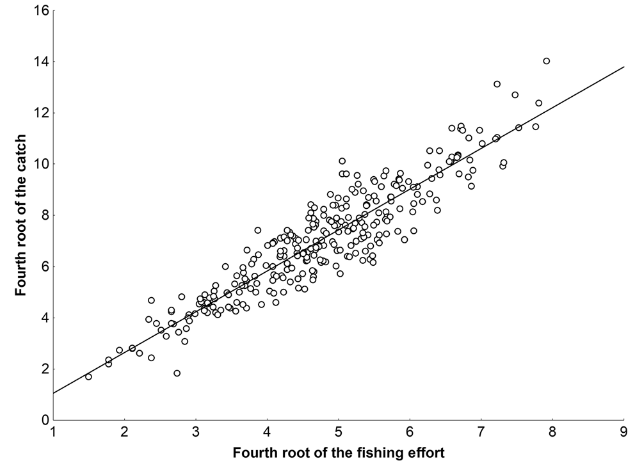

Fig. 2 Relationship between the fourth root transformation of the catch (**c**, originally measured in kg) and fishing effort (**f**, originally measured in fisher*day), where $\sqrt[4]{\mathbf{c}} = -0.38 + 1.74\sqrt[4]{\mathbf{f}}$ (s_α = 0.150; $t_\alpha = -2.536$; p = 0.012 and $s_\beta = 0.037$; $t_\beta = 47.465$; $p < 0.001$)

isolated, shallow lakes form in the low-lying areas during the dry phase (Petrere Jr. et al. 2007). When the river water level rises, the forest is flooded and the lakes become connected to the main channel of the Amazon River (Junk 1984), transforming the várzea into an extensive flooded system (Hess et al. 2003).

Fisheries in the study area support local, regional, and national economies. At the time of this study, fishermen typically exploited floodplain lakes mostly using gill nets, hooks-and-line, and seine nets deployed from motorized canoes and wood boats (Isaac et al. 2008). The total catch landed in cities of the region fluctuates between 5000 and 6000 t year^{-1} (Ruffino et al. 2005). Fishing accounts for about 40 % of household incomes of riverbank communities and 84 % of these households have some member that participates in fishery activities (Almeida et al. 2001). Santarém is the main landing port and trade market in the region, and no differences are expected between ports along the main river channel in the fishery patterns except for the number of landings.

Data sampling

We used commercial fisheries data collected under the auspices of two projects: The Middle Amazon Fishery Resources Administration (Iara/IBAMA), and the Natural Resources of the Várzea Management (ProVárzea/IBAMA). These projects used census methods to produce a comprehensive fisheries dataset. Catch and fishing effort data from each trip were recorded daily (except on Sundays) between January 1993 and December 2004, through interviews with boat owners or captains at the landing time. For all fishing boats landing in all the ports of the studied area, the following information was recorded: catch per fish species during the trip, type of vessel used (boat or canoe), environment (river or lake) fished, fishing gear, date and place of departure and arrival, number of fishermen in the trip, and number of days fishing.

Hydrological data came from the Hydrological Information System (HidroWeb) for 1993–2004 (http://hidroweb.ana.gov.br/), specifically for the municipality of Óbidos. We considered two hydrological metrics: the average monthly water level (in cm) and the average maximum monthly water level. For clarity, such metrics were obtained by a set of limnimetric scales placed across a transversal section of the river, standardized according to the sea level (ANA 2012).

Statistical analysis

We filtered the fisheries data to include only fishing trips data associated with gillnets and motorized boats (see Isaac et al. 2004) in order to reduce heterogeneity in catchability (Petrere Jr. et al. 2010). We also only included fishing trips in which the total catch of *P. nigricans* was at least 40 % of the total catch in weight (see Cruz et al. 2017). In doing this filtering, we assumed that all fishing trips in the resulting dataset included cases where *P. nigricans* was a target species. This resulted in 5548 fishing trip records in which *P. nigricans* accounted for 66 % of the total catch.

Preliminary analyses considered the possibility of using catch per unit effort (CPUE) as a catch index of abundance. We assessed if the relationship between catch (**c**) in weight (kg) and effort (**f**) measured in fisher*day was linear and if the regression line passed through the origin (strict proportionality; Petrere Jr. et al. 2010). But the regression line did not pass through the origin (Fig. 2), so our analyses focused on **c** as the main response variable.

To understand the intra-annual relationship between monthly river water levels and monthly catches of *P.*

nigricans over time, we evaluated the effect of river water levels on the catch of *P. nigricans* using an analysis of covariance (ANCOVA), considering monthly catches as a response variable. As explanatory covariates, we considered **f**, maximum monthly river water level, type of environment fished (river and lake), and year of fishing. The year factor was used as a proxy, which is a variable used to discount the effect of other commonly unknown variables that were not included in ANCOVA, such as the El Niño effect and effect of market oscillation over time. All variables were transformed into the fourth root to ensure the assumptions of normality of errors, verified through quantile-quantile plots with simulated envelope and the Shapiro-Wilk test. The homoscedasticity of variances was assessed visually via a scatter plot of the studentized residuals versus adjusted values in the standard range (− 3, 3). To assess the relative importance of each covariate in terms of its influence on **c**, we readjusted the ANCOVA model using standardized covariates (**Z**). The standardized covariates (**Z**) were calculated for the data on catches, fishing effort, average and maximum monthly river water levels, for all years, by dividing the differences between the data for each month (**x**) and the respective average ($\bar{\mathbf{x}}$) of the series by the respective standard deviation ($\mathbf{S_x}$). These analyses were done using R version 3.3.2 (R Core Team 2016).

To assess the inter-annual lag associated between monthly river water levels and monthly catches of *P. nigricans*, we used the standardized covariates (**Z**) in a cross-correlation function (CCF). CCF uses a series of correlation analyses to comprehensively assess for temporal lags between a possible explanatory variable (i.e., average monthly water level) and a response (i.e., catch, fishing effort; Legendre and Legendre 1998). CCF is given by the following equation:

$$\mathbf{r_{xy}(k)} = \frac{\mathbf{c_{xy}(k)}}{\mathbf{S_x(k)S_y(k)}} = \frac{\sum_{t=1}^{n-k}(\mathbf{x_{t+k}} - \bar{\mathbf{x}})(\mathbf{y_t} - \bar{\mathbf{y}})}{\sqrt{\sum_{t=1}^{n-k}(\mathbf{x_{t+k}} - \bar{\mathbf{x}})^2 \sum_{t=1}^{n-k}(\mathbf{y_t} - \bar{\mathbf{y}})^2}}$$

Where $\mathbf{r_{xy}(k)}$ is the cross-correlation coefficient; $\mathbf{c_{xy}(k)}$ is the coefficient of cross-covariance; $\mathbf{S_x(k)}$ and $\mathbf{S_y(k)}$ are the standard deviations of the respective series; $\mathbf{x_t}$ and $\mathbf{y_t}$ are the time series; $\bar{\mathbf{x}}$ and $\bar{\mathbf{y}}$ are the averages; **k** is the lag coefficient between the series ($\mathbf{k} = 0, \pm1, \pm2, \pm3, \ldots$); **n** is the number of observations. Our cross-correlation analysis was performed using PAST® 3.10 (Hammer et al. 2001).

Results

We found that the intra-annual relationship between monthly river water levels and monthly catches of *P. nigricans* over time was negative. Our final model had global significance ($F = 11.63$; $p < 0.001$) and explained 90% of the catch of *P. nigricans*. Catch was significantly related to fishing effort ($F = 1{,}311.12$; $p < 0.001$), maximum monthly river water level ($F = 56.19$; $p < 0.001$), type of environment ($F = 33.87$; $p < 0.001$), and year of landing ($F = 5.15$; $p < 0.001$; Table 1). The residuals were normally distributed ($W = 0.99$; $p = 0.93$), and randomly distributed around zero, showing no discernible trends and indicating that the variance was homogeneous. The estimates of the model parameters adjusted with standardized covariates (**Z**) indicated that the most important covariate for the adjustment of the ANCOVA model was fishing effort, followed by year and environment factors and maximum monthly river water levels in no clear order of magnitude of effect (Table 2). Environment, year, and maximum monthly river water levels thus had substantial effects on monthly catch, denoting both intra- and inter-annual effects of hydrological variability on catch of *P. nigricans*. The negative relationship between catch and maximum monthly river water level is clearly observed in Fig. 3.

We also found that the inter-annual lag associated between monthly river water levels and monthly catches of *P. nigricans* was of 15 months. The CCF analysis showed that catches and fishing effort were influenced by monthly variability in river water levels, as indicated by a moderate and positive correlation between average monthly river water level and monthly catch ($r = 0.40$), as well as average monthly river water level and fishing effort ($r = 0.44$). The most significant correlation occurred with a lag of 15 months ($p < 0.001$) for both catch and fishing effort (Fig. 4). These results indicate that the catch and fishing effort in any given month or year vary in response to hydrological variability occurring 15 months before.

Discussion

Our results showing a negative intra-annual relationship between monthly river water levels and monthly catches of *P. nigricans* highlight the dynamics of floodplain fisheries whereby flood pulses regulate the effectiveness of fishing

Table 1 ANCOVA results on the capture of *Prochilodus nigricans* from the lower Amazon region between 1993 and 2004

	df	SQ	F	p
Intercept	1	5.56	11.63	**< 0.001**
Fishing effort	1	627.22	1311.12	**< 0.001**
Maximum river water level	1	26.88	56.19	**< 0.001**
Type of environment	1	16.21	33.87	**< 0.001**
Year	11	21.14	5.15	**< 0.001**
Residual	271	129.64		

Significant variables ($p < 0.05$) are highlighted in bold (df = degrees of freedom; SQ = sum of squares) and F stands for the Fisher statistic value

Table 2 Parameters of the final model and with the data transformed into standardized variables (**Z**), or score variable, with standard errors, t-test, and p-values

Exploratory Variables	Final model parameters				Model parameters (**Z**)			
	Coef	SE	t	p	Coef	SE	t	p
Intercept	6.99	0.15	46.26	**< 0.001**	1.61	0.47	3.31	**< 0.001**
Fishing effort	2.14	0.06	36.21	**< 0.001**	**1.69**	0.05	36.21	**< 0.001**
Maximum river water level	– 0.32	0.04	– 7.50	**< 0.001**	– 0.56	0.07	– 7.50	**< 0.001**
Factor (Year) 1994	0.44	0.20	2.22	**0.03**	0.44	0.20	2.22	**0.03**
Factor (Year) 1995	– 0.15	0.20	– 0.73	0.46	– 0.15	0.20	– 0.73	0.46
Factor (Year) 1996	– 0.14	0.1930	– 0.71	0.48	– 0.14	0.1930	– 0.71	0.48
Factor (Year) 1997	– 0.71	0.20	– 3.50	**< 0.001**	– 0.71	0.20	– 3.50	**< 0.001**
Factor (Year) 1998	– 0.45	0.20	– 2.26	**0.02**	– 0.45	0.20	– 2.26	**0.02**
Factor (Year) 1999	0.06	0.20	0.30	0.76	0.06	0.20	0.30	0.76
Factor (Year) 2000	– 0.42	0.19	– 2.10	0.36	– 0.42	0.19	– 2.10	0.36
Factor (Year) 2001	– 0.35	0.20	-1.75	0.08	– 0.35	0.20	– 1.75	0.08
Factor (Year) 2002	– 0.40	0.20	– 1.95	0.05	– 0.40	0.20	– 1.95	0.05
Factor (Year) 2003	– 0.65	0.20	– 3.20	**0.001**	– 0.65	0.20	– 3.20	**0.001**
Factor (Year) 2004	– 0.46	0.21	– 2.18	**0.03**	– 0.46	0.21	– 2.18	**0.03**
Factor (Environment) river	0.61	0.10	5.82	**< 0.001**	0.61	0.10	5.82	**< 0.001**

Values significantly lower than 0.05 are highlighted in bold. The bold value of the t-test for fishing effort indicates that it was the most important covariate for explaining the catch of *Prochilodus nigricans* from the lower Amazon region between 1993 and 2004

SE standard error; *Coef* coefficients

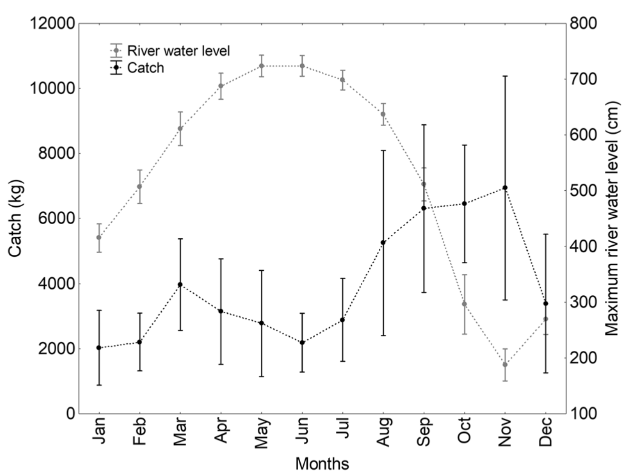

Fig. 3 Relationship between the monthly catch of *P. nigricans* and the maximum monthly level of river water from lower Amazon region between 1993 and 2004. The vertical bars represent 95 % confidence interval

gears and associated catches. During the flood, adults of the *P. nigricans* access flooded areas to replenish the energy spent during the spawning period (Montreuil et al. 2001; Silva and Stewart 2017) as their larvae and fingerlings find abundant food and shelter until the juvenile phase (Araújo-Lima and Oliveira 1998). The submerged vegetation provides refuge areas from predators and high availability of food resources increase survival rates of larvae, young, and adult *P. nigricans* (García et al. 1997; Araújo-Lima and Oliveira 1998; Winemiller and Jepsen 1998; Silva and Stewart 2006). During this period, fishing gears face decreased efficiency (Valderrama et al. 1993), as fish are dispersed in a large flooded environment. The largest catches observed during the receding water and low water months result from the reduction in the water volume, making fish more vulnerable to fishing gear (Barthem and Fabré 2004; Mota and Ruffino 1997; McGrath et al. 2005). During the receding period of water levels, *P. nigricans* form schools to move towards the main channel of the Amazon River, passing through narrower channels (Fernandes 1997), at which time they are caught by fishing gears (Valderrama et al. 1993). During low water periods, there is a clear definition in the periodicity of catches with a very high yield in these months (Isaac et al. 2004). Fishers seek to maximize their profit by moderating elements of their effort, for example, using the most appropriate boat, equipment, labour or fuel to attain a profit (Almeida et al. 2012).

Our results showing positive correlations with a 15-month lag between river water levels and catches of *P. nigricans* indicate that, if a year is characterized by a very high river water level compared to the average, the catch will also increase 15 months later. This lag after intense floods should be directly linked to increased survival and growth rates of *P. nigricans*, favoured by the higher heterogeneity of habitats and food supply (Bayley et al. 2018), owing to increased extension and connectivity between water and forest (Hurd et al. 2016). Increased habitat availability increases the diversity and availability of potential refuges

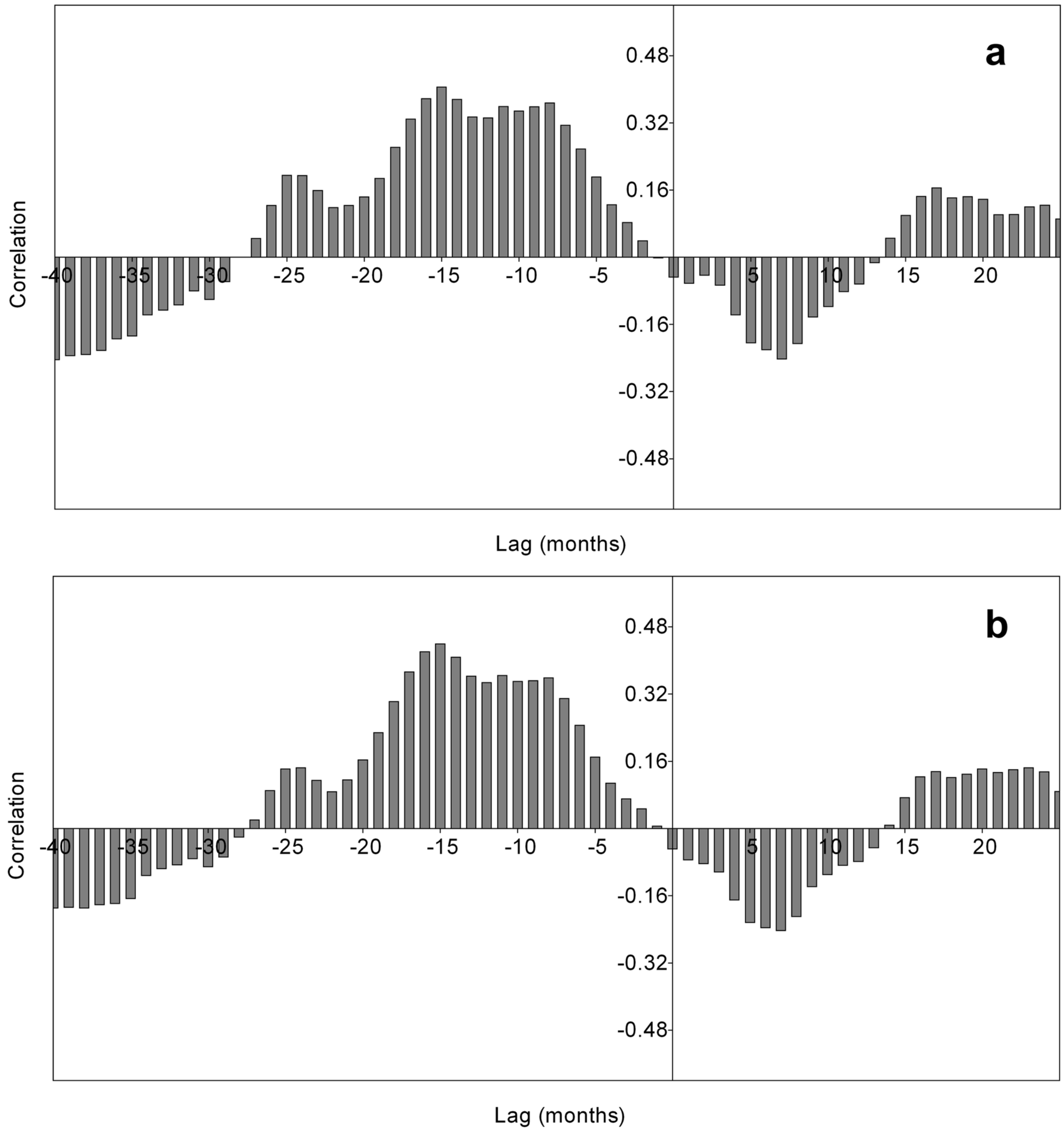

Fig. 4 Cross correlation of (**a**) catch and (**b**) fishing effort as a function of average river level

from predators (Goulding 1980; Mérona 1990), which might lead to increased reproductive success and decreased natural mortality rates (Araújo-Lima and Oliveira 1998; Montreuil et al. 2001; Isaac et al. 2008; Fabré et al. 2017). In addition, the larger the flooded area, the higher the access of fish to resources such as phytoplankton and detritus (Araújo-Lima and Oliveira 1998; Silva and Stewart 2006). That likely would increase body growth and, thus, biomass of the fish population (Fernandes 1997; Castello 2008).

Our inter-annual lag results appear to complement previous studies on the effects of hydrological variability on *P. nigricans*. Bayley et al. (2018) showed that the *P. nigricans* population at 29 months of age was positively related to flooding extent measured in terms of the 'moving littoral' (i.e., the littoral feeding area of *P. nigricans*), even though they did not find any relation to catch, as showed here. According to Santana and Freitas (2013), there is no fishing pressure on the younger age groups of *P. nigricans* in the lower Amazon, as catches are directed to fish aged 2 years or older. If *P. nigricans* recruits to the fishery at age two in our study area, which is plausible (e.g., Bayley et al. 2018), a 15-month lag could represent the interval between hydrological variability and its effect on age-three abundance when the fish are harvested. In the central Amazon, the proportion of numbers of *P. nigricans* caught by age class is relatively the same for age classes two, three, and four (Bayley et al. 2018). Therefore, as suggested before, the intensity of flood events increases recruitment (Mérona and Gascuel 1993; Bayley et al. 2018; Castello et al. 2019b), but their effects will only be noticed in fish catch in subsequent years (Santana and Freitas 2013; Castello et al. 2015; Isaac et al. 2016).

Considering that *P. nigricans* needs to remain for at least 15 ss in floodplain environments, ongoing changes in the hydrological cycle of the Amazon River, which mostly involve increasing the severity of low water (i.e., droughts), may be expected to adversely affect catches in the future. As shown by our results, decreased water levels would tend to decrease fish catches. This developing form of hydrological alteration represents a threat to the food and income securities services provided by populations of *P. nigricans* (Mérona and Gascuel 1993; Halls and Welcomme 2004; Fabré et al. 2017; Begossi et al. 2019). Future research is necessary to assess the extent to which such hydrological changes (Welcomme et al. 2010) can affect multispecies fisheries catches when in conjunction with increased levels of fishing effort. Hydrological alterations affect the survival of fishery species, especially during the early stages of development, owing to a lack of shelter from predators and food shortages, which may interfere with their reproductive success (Silva and Stewart 2017). Therefore, it is evident that limiting current levels of fishing exploitation while minimizing hydrological alterations are fundamental for maintaining the fishery yields of *P. nigricans* in the future.

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Code availability Not applicable.

Compliance with ethical standards

Conflict of interest All authors declare that there were no conflicts of interest.

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