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What makes a good catch? Effects of variables from individual to regional scales on tropical small-scale fisheries

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ABSTRACT

Small-scale fisheries are vital for millions of people worldwide, but hard to monitor and manage. We investigated the effects of variables related to different spatial scales and theoretical backgrounds, from protected areas (PA) to individual decision-making, on parameters of small-scale fisheries (catch, effort, and catch per unit of effort - CPUE) in the Tapajós and Negro rivers, Amazon. Although both individual- and large-scale variables affected fish landings, the former group was more important. Fish sales, group fishing, and the fishing technique used were the most important variables affecting all parameters. Number of activities performed and time traveled to fishing spot influenced effort and catch. Education level was negatively related with effort. At the large-scale, fishing effort and catch were higher outside PA. Distance to the urban center was positively related with CPUE. Large-scale predictors of fishing yields could help to define broader management goals, while variables at the individual-level may help to identify vulnerable groups to changes in fisheries and to adjust management to minimize conflicts, improving acceptance and compliance.

1. Introduction

Small-scale fisheries encompass the majority of fisheries conducted in developing countries (FAO, 2014). These fisheries can be highly productive and have an important role in the income and food security of riverine populations (Bené et al., 2009). However, despite their importance to prevent and alleviate poverty, small-scale fisheries are usually neglected by political and economic projects (Lynch et al., 2017). The lack of data, statistics, and scientific studies for small-scale fisheries are also of major concern. Estimates indicate that 65% of the household consumption of freshwater fish in low-income countries is not officially reported (Fluet-Chouinard et al., 2018). In this sense, small-scale fisheries may cause impacts on fish communities, such as decreasing the abundance and size of target fish (Allan et al., 2005) and disrupting valuable ecosystem services, including food and protein provision (Golden et al., 2016).

Small-scale fisheries are complex socioecological systems (Begossi et al., 2012) and fishing yields may be influenced by several factors operating at multiple scales. Management strategies in small-scale fisheries occur at different decision levels: regional (broad scale, including state and federal levels), local (i.e., communitarian), and individual (Castro and McGrath, 2003; Maccord et al., 2007; Fulton et al., 2011). A better understanding of which factors most influence fishing yields and fishing effort can contribute to understand fishers' behavior and to devise management measures aimed to regulate fishing effort without drastic reductions on fishing yields (Hallwass et al., 2013). At a broad spatial scale (regional level), there is an ever growing evidence that protected areas (PAs) increase the size and abundance of fish and their availability to fisheries in both marine (Halpern, 2003) and freshwater environments (e.g., Sanyanga et al., 1995; Keppeler et al., 2017); however, the latter is far less studied (Chessman, 2013). Also at a regional scale, recent studies indicate a negative effect of proximity to large cities on fish abundance and fish sizes (Brewer et al., 2012; Cinner et al., 2012; Tregidgo et al., 2017; Keppeler et al., 2018). This could lead to an inverse relationship between distance to cities and fishing yields, possibly due to anthropogenic impacts on fish near cities, including excessive fishing, deforestation, farming, pollution, among others.

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Two major theoretical approaches could be applied to explain variations in fishing yields at the level of the individual fishers. First, fishers' behavior may be influenced by socio-economic pressures and by the need to adjust fishing strategies in face of stock fluctuations and local environment conditions. Fishing strategies are usually mediated by the local ecological knowledge (LEK) of fishers (Fulton et al., 2011; Silvano and Begossi, 2012; Huntington et al., 2017). Basic education may also influence the behavior of fishers (Muallil et al., 2011) given its capability of reducing the chance of systematic errors in judgment and decision-making of individuals (Kim et al., 2018). However, although fishers' LEK and education could lead to improved management strategies or increased fishing yields (Berkes et al., 2000; Silvano and Begossi, 2002), to our knowledge these relationships have not been empirically demonstrated nor tested.

Second, the optimal foraging theory (OFT) and derived models have been applied to understand the behavior of animals, including humans, related to resource use, diet choice, among other aspects (e.g., Lieberman, 2006; Lopes et al., 2011). The OFT models predict that a given forager would maximize returns (e.g., catch) while minimizing costs (e.g. time spent foraging; Lopes et al., 2011). The optimal foraging models have been applied to understand fishers' behavior with mixed results (Begossi, 1992; Aswani, 1998; Lopes et al., 2011). According to the central place model derived from OFT, a fisher that needs to return to a central place (home or market) would increase the catch and effort when traveling to more distant fishing spots, to compensate for increased travel costs (Oliveira and Begossi, 2011). Fishers are also expected to maximize fishing returns by selecting the most efficient fishing techniques (Begossi, 1992; Aswani, 1998) and by choosing an optimal crew size and composition (Hallwass et al., 2013). Depending on fish demand and availability, and local rules, fishers may also consider to focus all their time on fisheries or have multiple economical activities (Cinner and Bodin, 2010). The strategy adopted, either specialization or diversification, are likely to determine the fishers catch and effort, given that specialized fishers may need to fish more to trade or sell their catch for other goods (Salas and Gaertner, 2004; Cinner and Bodin, 2010; Hallwass et al., 2013).

Over the last decades, there has been a shift in the view of how fisheries' management programs should be established, from a more government-centered approach (regional or national scale) to a more decentralized one at the communitarian (local) scale (Pomeroy and Berkes, 1997). Nevertheless, the relative influences of factors operating at distinct scales on fishing yields or fishing effort are not well known, especially for tropical freshwater fisheries, such as in the Amazon Basin. Fish is the main animal protein consumed by riverine communities in the Amazon and provide employment and income for more than 500,000 people in the region (Begossi et al., 2019). Amazonian small-scale fisheries are characterized by the use of multiple fishing gears and involve multiple fish species captured in different habitats (Bayley and Petrere, 1989; Castello et al., 2013). Signs of overexploitation have already been found in some fish populations (e.g., Petrere et al., 2004; Garcia et al., 2009). Indeed, an anthropogenic gradient can be observed in fish communities, as the presence of large fish is positively related with distance to urban centers, possibly reflecting the influence of commercial fishing activity (Tregidgo et al., 2017; Keppeler et al., 2018). In the Amazon basin, PAs are one of the main tools for biological conservation at the regional scale, but the effects of these regional management measures to improve fisheries are not well known (Keppeler et al., 2017). Co-management has been also widely applied, mostly in the form of fishing agreements (Oviedo et al., 2015), or in communities located within PAs that alllow the sustainable use of natural resources (Maccord et al., 2007; Silvano et al., 2014). Nevertheless, in a complex socioecological system such as the Amazon basin, where some of the main fish species exploited are highly mobile and may undertake long migrations (Petrere et al., 2004), management plans may be needed at multiple scales (Hallwass and Silvano, 2016).

Because of their heterogeneity regarding fishing gears used, habitats and fish species exploited and management strategies (PAs and local rules), the Amazonian fisheries could be a good case study to evaluate the influence of factors at distinct scales on fishing yields. The Amazonian fisheries also have similar problems shared with many tropical small-scale fisheries, such as heterogeneity, logistic restrictions and lack of financial resources to support surveillance and enforcement (Prince, 2003; Maccord et al., 2007). The identification of factors that influence fishing yields the most could contribute to evaluating the potential effects of alternative management measures not only on fish stocks, but also on fishers' livelihoods (Hallwass et al., 2013). Altough there are evidences of the relevance of some of these factors, such as PAs or optimization (see above), to our knowledge these major theoretical approaches to explain fishing yields have not been compared with the same dataset, as such comparison would require a refined level of detail in fisheries data.

Our main goal is to investigate the relative effects of ten explanatory variables related to different spatial scales on fishing yields (catch, effort, and catch per unit of effort - CPUE) in two large tropical rivers in the Amazon Basin. We evaluated variables representing four main theoretical approaches: two variables at the regional scale (representing influence of PAs and distance to urban centers) and eight variables at the individual scale (representing optimization behavior and fishers' knowledge), besides five confounding variables related with the environment, and fishers' and communities' identity (Table 1). We compared the effects of all these variables and their underlying theoretical backgrounds through a model averaging approach, which indicate those variables (and models) that influenced most the fishing yields and effort. We thus addressed two major questions: 'Which variables, and at which scale, would influence most the fishers' catches and fishing effort?' 'Do the same variables influence fishing yields and effort?' If yields and effort are related to distinct variables, managers and fishers themselves could apply this information to devise management rules that could reduce fishing effort without affecting fishing yields, in a win-win approach.

2. Material and Methods

2.1. Study area

The study was conducted with artisanal fishers of the Lower Tapajós River and Middle Negro River, two of the seventeen tributaries of the Amazon river with more than 1,500 km of extension. The Amazon basin is located in the territories of Brazil, Bolivia, Peru, Ecuador, Colombia, Venezuela, Guyana, Suriname and French Guiana, and the two studied rivers are located in the Brazilian territory. The Lower Tapajós River (Lat: -3.60 to -2.34, Long: -55.19 to -54.90) has clear oligotrophic waters with low conductivity and pH close to neutral (Goulding et al., 2003). The Middle Negro River (Lat: -2.41 to -1.55, Long: -62.65 to -60.98) has black waters with low nutrient levels, low pH values and large quantities of dissolved organic matter. Both rivers have seasonally inundated floodplains that connect aquatic habitats, such as lakes, channels, and the main river, during the wet season (Sobreiro et al., 2010; Keppeler et al., 2017). A previous study indicated that fish abundance (mean catch rates of fish through experimental fishing) in the Lower Tapajós is lower than in the Middle Negro River (0.54 g m^{-2} h^{-1} and 2.69 g m^{-2} h^{-1}, respectively; Keppeler et al., 2017). More information on the environmental characteristics, fish, and fisheries of each river can be found in previous studies (Begossi et al., 2005; Silva and Begossi, 2009; Keppeler et al., 2017, 2018).

In this study, we followed the IUCN definition of PA, which is considered as "a clearly defined geographical space, recognized, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values" (Dudley and Stolton, 2008). Following this definition, the Lower Tapajós River has two main PA: The Tapajós National Forest created in 1974 and the Tapajós-Arapiuns Extractive Reserve

Table 1
Rationale and description of each variable used to explain catch (kg), catch per unit of effort (CPUE), and effort (hours) of fish landings in the Tapajós and Negro River, Brazilian Amazon. The theoretical background and reference for the rationales are in the Introduction section. Confounding variables were considered as random variables in the analysis.

Variable	Factor level	Scale	Rationale (hypothesis)
Protected area (PA)	Categorical (inside or outside)	Regional	PAs are associated with higher catch and CPUE, and lower fishing pressure
Distance to urban center	Continuous (km)	Regional	Distance is positively related with catch and CPUE
Fishing technique	Categorical (angling, castnet, gillnet, longline, and spear fishing)	Individual	Optimization: choice of fishing gear that provides higher yields
Fish sales	Categorical (yes or no)	Individual	Optimization: higher effort, catch and CPUE when the fisherman's goal is to sell the fish he/she caught
Group fishing	Categorical (yes or no)	Individual	Optimization: higher catch and CPUE when fishing in groups
Time to fishing spot	Continuous (hours)	Individual	Optimization: catch and fishing effort are positively related to time traveled to fishing spot
Number of activities	Categorical (1, 2, 3, or 4)	Individual	Optimization: Higher number of activities exerted reduce fishing effort
Age	Continuous (years)	Individual	Experience and knowledge*: age positively relates to catch and CPUE
Time living in the region	Continuous (years)	Individual	Experience and knowledge*: time positively relates to catch and CPUE
Education	Categorical (uneducated, elementary, middle, or high school)	Individual	Experience and knowledge*: Higher levels of basic education lead to higher fishing yields
Season	Categorical (raising, low, high, or falling water)	Regional	Confounding variable
River	Categorical (Tapajós or Negro)	Regional	Confounding variable
Habitat	Categorical (*igarapé*, lake, or river)	Local	Confounding variable
Riverine communities	Categorical (several levels)	Local	Confounding variable
Fisher ID	Categorical (several levels)	Local	Confounding variable

* Age and time living in the region were considered to be related with local ecological knowledge (fishing experience), whereas education was considered to be related to formal knowledge (technical skills provided by schools). Exploratory analysis indicated weak or absent correlation between ecological knowledge (age and time living in the region) and formal knowledge (education).

created in 1998. In the Middle Negro River, there are three main PA: Unini River Extractive Reserve created in 2006; Jaú National Park created in 1980; and Anavilhanas National Park that was created as an Ecological Station in 1981 and became a National Park in 2008. The presence of riverine communities is common in all these PA, except in Anavilhanas, and the locals rely on several economic activities, including subsistence agriculture, farming of small animals, extraction of forest products, hunting and artisanal fisheries (Sobreiro et al., 2010; Keppeler et al., 2017). Larger scale commercial fishing is not allowed within PA and buffer zones. Human density is usually higher in surrounding unprotected areas (herein called non-PA), where the fishing is more intensive, especially in the Lower Tapajós region (Keppeler et al., 2017).

2.2. Interviews and fish landing

Data were obtained from interviews with fishers and fish landing records in two separate research projects, each one conducted year-round. One project conducted in the Tapajós River from July 2013 to June 2014, and the other conducted in both the Tapajós and Negro rivers from June 2016 to May 2017. According to data collected by the Brazilian Water Agency, these two annual cycles were similar in terms of water level (Fig. A.1). Water level is usually related with fish catch and effort and can be a confounding effect in fisheries analyses. Furthermore, the researchers (RAMS and GH) responsible for the visits to the riverine communities and the interviews were the same in both projects, reducing potential sampling bias. Exploratory analysis also indicated that inter-annual variance was weak and not relevant for the purpose of this study, as the time difference was short (two years only). Therefore, we decided to combine and analyze these two datasets together, to get a larger sampling size.

Interviews were conducted in sixteen riverine communities in the Lower Tapajós River, where eleven of these communities were located within PA (four in the Tapajós National Forest and seven in Tapajós-Arapiuns Extractive Reserve) and five were located in a non-PA (Fig. A.2). Interviews were also conducted in eight riverine communities in the Middle Negro River; one was located in the Anavilhanas National Park, two in the Jaú National Park, two in the Rio Unini Extractive Reserve, and three in non-PA. The riverine communities selected are similar to others in the two studied rivers, which are generally composed by a small number of families of mixed origin (indigenous, afro-descendants, and caucasians), low educational level and low mean wage. Within each riverine community, a snowball sampling procedure (Hallwass et al., 2013) was conducted to select fishers to participate in the study. Information used in this study regarding experience (age, time living in the region), economic activities (fisheries, farming, etc.), and socioeconomic profile (education, gender, etc.) were obtained from individual interviews, which lasted between 20 to 40 minutes each following a standardized semi-structured questionnaire (Table A.1; Keppeler et al., 2017).

After the initial interview of 484 fishers, those that fish at least three days per week were invited to voluntarily record their fish landings (i.e., catch of their fishing trips). Those fishers that agreed to record their fishing received a set of materials, including hanging scale and forms, and a brief training to register the first five fisheries of each month. The training was conducted with the participating fishers and occasionally with members of their families, who often assist fishers to fill the forms. During this training, we simulated the filling of the fishing forms to explain to fishers how the data should be recorded and to serve as a practical example, in case fishers had doubts about filling the survey. After each fishing trip, fishers were oriented to inform the location (lake, river or small streams) and time to arrive in the fishing spot, fishing technique (angling, spear fishing, longline, gillnet or cast net), time spent fishing (hours), number of fishers in the crew, catch (kg), and if the fish was sold or consumed (Table A.2). A catch was considered sold even if just a fraction of this catch was sold to the markets. Therefore, this variable (fish sale) is an explanatory variable related to fishers' behavior (propensity for selling the catch). When possible, phone calls were made to check fishers' engagement to the study and answer potential questions. Fish landing forms were collected every three months. It is important to note that, although some may engage in other secondary activities, fishers who participated in this study depend on fisheries as their main economic activity.

2.3. Distance to the main urban center

The software GOOGLE EARTH PROFESSIONAL was used to calculate the riverine distance (km) between riverine communities and the closest urban center (Santarém – Lower Tapajós River, Manaus – Middle Negro River). The distance measurements were conducted in a height of approximately 75 km using Landsat images (30 m resolution) taken in December of 2016 (end of the dry season).

2.4. Data processing

A total of 5,771 fish landings (Negro River = 1,492, Tapajós River = 4,279), obtained by 222 fishers in 24 fishing communities, were recorded during the study period (Table A.3). However, given the uncertainty in many recordings (not specified or multiple options selected) about the values of the dependent variables of interest, the site where the fish were caught and the fishing technique utilized, we used a subset of the data including nineteen fishing communities (eleven in the Tapajós River and eight in the Negro River; Fig. A.2) that totalized 2,573 fish landings (104 fishers) for catch analysis, 2,543 fish landings for nominal (raw) CPUE (102 fishers), and 2,578 fish landings for effort (106 fishers). For the number of activities (available for the Tapajós River only) and time to fishing spot, the data available was more scarce (N = 1,964 and N = 785, respectively) and we analyzed each one separately.

2.5. Data analyses

Random intercept linear mixed-effects models (LMM) were used to verify how the dependent variables catch (kg), effort (hours) and CPUE, calculated as catch/ (N of fishers * effort), respond to the effect of the independent variables: PA (inside or outside), distance to urban center, fishing technique, age, education, time living in the region, fish sales (yes or no), and group fishing (yes or no) (Table 1). We considered effort as a response variable given its possible dependence on processes at the regional (e.g., management rules), local (e.g., fishing agreements) and individual scales (e.g., fisher experience, socio-economic status). The random structure of the model was defined following Zuur et al. (2009), which suggests that a beyond optimal model should be fitted to the data with as many variables as possible. Then, keeping the main independent variables constant, the random structure of the model is switched and compared using the AIC criterion. We created models with up to five random variables: season, habitat, river, riverine communities, and fisher identity; the last three variables listed were structured in a nested fashion (i.e., river/riverine communities/fisher identity). We considered these variables as random variables due their potential confounding effects on the response variables and also to account for the lack of independence among fishing landings from the same fishers. For the analyses of catch and CPUE, the random component of the model selected (i.e., model with the lowest AIC) contained the variables season and fisher (Table A.4). For the effort, the best random structure was the one encompassing riverine communities/ fisher and season (Table A.4).

After the selection of the random structure of our models, a model averaging procedure (Burnham and Anderson, 2002) was used to obtain relative importance values (*I,* which varies from zero to one, the larger the value, the more important it is) and robust estimates of the parameters (including confidence intervals - CI) of all the main variables of interest: PA, distance to urban center, fishing techniques, age, education, time living in the region, fish sold and group fishing. PA, fishing techniques, education, fish sold and group fishing were considered as categorical variables, while distance to urban center, age and time living in the region were considered as continuous variables (Table 1) having a linear relationship with the response variables (i.e., no polynomial term was added in the models). Interaction terms were not included in the analyses. The model averaging analysis was preferred instead of a classic model selection because the differences between the best model and the other model candidates were usually small.

Since the data available for the number of activities (available for the Tapajós River only) and time to fishing spot was more limited, we analyzed their effects on catch, effort, and CPUE separately. More specifically, we used the most important variables according to the model averaging procedure as co-variables and then tested if the inclusion of the variable of interest significatively explained each of the three dependent variables. The significance of these three variables was assessed using a parametric bootstrap method (Halekoh and Højsgaard, 2014). Number of activities was considered as a categorical variable, while time to fishing spot was considered as a continuous variable with a linear relationship with the response variables.

Multicollinearity was verified in the data using the variance inflation factor (VIF), which indicated low correlation among the predictors (VIF < 2.5), except for the number of activities exerted and fish sales. In this case, we decided to test the effect of the number of activities exerted without the presence of fish sales and then interpret the results with this autocorrelation in mind. Dependent variables and the independent variable time to fishing spot were log-transformed before analysis to meet model assumptions of normality and homogeneity of variance (Fig. A.3). To quantify the goodness of fit of the best models, the marginal (variance explained by the independent variables) and conditional R^2 (variance explained by both independent and random variables) were calculated according to Nakagawa and Schielzeth (2013). Marginal effects (i.e. variation of the dependent variable according to a change in the predictor of interest while keeping all other predictors constant) based on the model averaging approach were used to interpret the influence of the independent variables on catch, effort, and CPUE. For the number of activities and time to fishing spot, the marginal effects were based on a single model.

The mixed models, model averaging procedure, and the parametric bootstrap were conducted in the R packages (R Core Team, 2018) lme4 (Bates et al., 2015), MuMIn (Barton, 2018), and pbkrtest (Halekoh and Højsgaard, 2014), respectively.

3. Results

An average of 24.7 (± SE of 22.33) fish landings was registered per fisher in both rivers. The catch per fish landing varied greatly, from 0 to 570 kg (average of 10.11 ± 20.36 kg). Fishing trips were usually short, lasting on average 4.32 (± 4.72) hours. The most used fishing techniques were gillnets (54.1%) and angling (21.4%). Almost 70% of the fish landings were originated from the main river. Just 27% of the fish landings reports indicated that fish was sold to neighbors or small markets. Fish sales were more common in non-PA (38.2% of fish landings) than PA (21.5%). The percentage of fish landings on which fishes were sold (i.e., fish catch was not consumed but sold to local markets or other members of the community) was more than two and a half times higher for specialized fishers (dedicated to fishing only) than for those of fishers involved with other economic activities (62% vs 24%, respectively). In most of the recorded fish landings, fishers fished alone (66.9%).

Local fishers were on average 39 years old (± 12.13). Excepting one out of 108 persons, all studied fishers were male. Most of them (64.8%) lived in the studied region since they were born. Forty-five percent of the fishers attended only elementary school, 26% completed middle-school, 8% high-school, and 20% did not attend school. Eighty-two percent of total fishers claim they have an extra economic activity in addition to fishing, the most common being farming (68.4%) and rubber tapping (12.3%). A summary of these variables organized by riverine communities can be found in Table A.5.

Group fishing, fish sale, and fishing technique were the most important factors to explain the variation found in all response variables studied (I = 1, Table 2). These factors were also present in the best models created (Table 3) and had coefficient intervals not encompassing zero (Fig. 1), which indicated consistency among models. Protected area was an important and consistent predictor in the best models of catch and effort, but not in models of CPUE (Table 2, 3;

Table 2
Relative importance of eight studied predictor variables (group fishing, fish sales, fishing technique, protected area, time living in the region, distance to urban center, age, and education), derived from a model averaging approach, to explain the variation of three response variables: catch (kg), effort (hours) and catch per unit effort (CPUE).

Predictor	Response variable		
	Catch	Effort	CPUE
Group fishing	1.00	1.00	1.00
Fish sale	1.00	1.00	1.00
Fishing technique	1.00	1.00	1.00
Protected area	0.96	0.95	0.17
Time living in the region	0.38	0.02	0.16
Distance to urban center	0.30	0.01	0.86
Age	0.10	0.02	0.27
Education	0.04	0.96	0.07

Fig. 1). Education was an important and consistent predictor of effort, while distance to urban center was an important predictor for CPUE (Table 2, 3; Fig. 1). Age and time living in the region were not informative predictors for any of the variables studied (Table 2, 3; Fig. 1).

Catch was mainly explained by four models that accounted for an accumulative weight of 0.95; all models included the variables PA, group fishing, fish sold, and fishing technique (Table 3). Catch was lower within PA (Fig. 2a), when angling technique was used (Fig. 2b), fisher was fishing alone (Fig. 2c) and fish was not sold (Fig. 2d). Mean condition R^2 (0.64) was more than two times the average marginal R^2 (0.28), indicating that the random variables explained a high percentage of the catch variation. According to the intercept values of the random variables, fishers differed in terms of catch, and catch values were higher during the low and falling water period (Fig. A.4).

Effort variation was explained primarily by five variables that were present in four main models (Table 2,3). Fishers in non-PA invested more time on fisheries than fishers in PA (Fig. 3a). Angling and long line techniques (Fig. 3b), group fishing (Fig. 3c), and the occurrence of fish sale (Fig. 3d) were all associated with higher fishing effort. A negative relationship between education and effort was also found (Fig. 3e). Mean condition R^2 was high when compared to marginal R^2 (R^2 = 0.61 vs R^2 = 0.17), suggesting high importance of random variables in explaining effort variation. The values of the random intercept coefficients indicated that effort was higher during high and falling water periods. Riverine communities and fishers also seem to have varied greatly in terms of fishing effort (Fig. A.4).

In relation to the CPUE, seven models encompassed 0.95 of the AIC weight and had an average marginal R^2 of 0.15 (Table 3). Four main variables were present in these models: distance to urban center, group fishing, fish sale, and fishing technique. Distance to the urban center was positively related with CPUE (Fig. 4a). Cast net, gillnets, and spearfishing had higher CPUE values than longline and angling techniques (Fig. 4b). Group fishing and the non-occurrence of fish sales were associated with lower CPUE values (Fig. 4c and d). PA was not considered an important variable according to our initial modeling averaging approach using environmental variables (river and season) as random variables. However, an extra analysis conducted to explore how the effect of PA differed among rivers indicated that fishing within a PA increased the fishers' CPUE in the Tapajós River (PBtest = 5.67, P = 0.01), but not in the Negro River (PBtest = 1.21, P = 0.28), indicating an interaction effect between River and PA (Fig. 5). Similar to catch and effort variables, high percentage of CPUE variation was explained by the random variables (average conditional R^2 of 0.5). Random intercept values indicated that CPUE is higher during falling and low water periods and that fishers productivity vary strongly (Fig. A.4).

Using models with a subset of the data, time to fishing spot was related positively with catch (PBtest = 19.67, $P < 0.01$, R^2 = 0.04, Fig. 6a), while the number of activities had a weak negative and marginally significant relationship (PBtest = 3.41, P = 0.06, R^2 = 0.03, Fig. 6b). Time traveled to fishing spot positively affected fishing effort (PBtest = 44.99, $P < 0.01$, R^2 = 0.05; Fig. 6c), while number of activities performed was negatively related with effort (PBtest = 15.70, $P < 0.01$, R^2 = 0.10; Fig. 6d). Finally, time to fishing spot (PBtest = 1.38, P = 0.22, $R^2 < 0.01$) and number of activities (PBtest = 0.99, P = 0.34, $R^2 < 0.01$) did not significatively affect the fisher's CPUE.

4. Discussion

The results showed that theoretical approaches operating at both regional (PAs and distance to cities) and individual (optimal foraging and education) scales are useful to understand fishing yields and effort. Nevertheless, the model comparisons indicated that variables at the individual level influenced more the catch, CPUE and effort of fish landings than regional variables. The explanation power of the variables of interest (i.e. independent variables) were generally low (Marginal $R^2 < 0.30$), however this is expected in complex and diverse socio-ecological systens, such as tropical rivers (e.g., Castello et al., 2018; Keppeler et al., 2018). Our findings are in agreement with other studies claiming that fishers' behaviour and socioeconomic characteristics may directly affect fisheries performance and success of fishery management (Aswani, 1998; Salas and Gaertner, 2004; Fulton et al.,

Table 3
Best models (accumulate weight lower than 0.95) according to the AICc criterion. Season and fishers were used as random variables for catch and CPUE models, while riverine communities, fishers and season were used as random variables for Effort models. For more details, see the data analysis section and Table A.3.

Models	AICc	Delta	Weight	Marginal R^2	Condition R^2
Catch					
Fishing technique + Group fishing + Time living in the region + PA + Fish sale	3,782.1	0.00	0.35	0.28	0.64
Dist. to urb. Cent. + Fishing technique + Group fishing + PA + Fish sale	3,782.5	0.38	0.29	0.27	0.63
Fishing technique + Group fishing + PA + Fish sale	3,783.2	1.06	0.21	0.28	0.64
Age + Fishing technique + Group fishing + PA + Fish sale	3,785.1	3.05	0.08	0.28	0.64
Effort					
Education + Fishing technique + Group fishing + PA + Fish sale	1,579.5	0.00	0.91	0.19	0.58
Education + Fishing technique + Group fishing + Fish sale	1,587.1	7.58	0.02	0.07	0.58
Age + Fishing technique + Group fishing + PA + Fish sale	1,588.0	8.47	0.01	0.19	0.56
Fishing technique + Group fishing + PA + Fish sale	1,588.1	8.59	0.01	0.24	0.73
CPUE					
Dist. to urb. Cent. + Fishing technique + Group fishing + Fish sale	2,042.9	0.00	0.32	0.14	0.49
Age + Dist. to urb. Cent. + Fishing technique + Group fishing + Fish sale	2,043.9	1.03	0.19	0.14	0.49
Dist. to urb. Cent. + Fishing technique + Group fishing + PA + Fish sale	2,044.4	1.58	0.15	0.15	0.50
Dist. to urb. Cent. +Fishing technique + Group fishing + Time living in the region + Fish sale	2,044.6	1.79	0.13	0.14	0.49
Dist. to urb. Cent. + Education + Fishing technique + Group fishing + Fish sale	2,046.0	3.16	0.07	0.15	0.50
Age + Fishing technique + Group fishing + Fish sale	2,046.3	3.47	0.06	0.15	0.50
Fishing technique + Group fishing + Fish sale	2,046.9	4.01	0.04	0.15	0.51

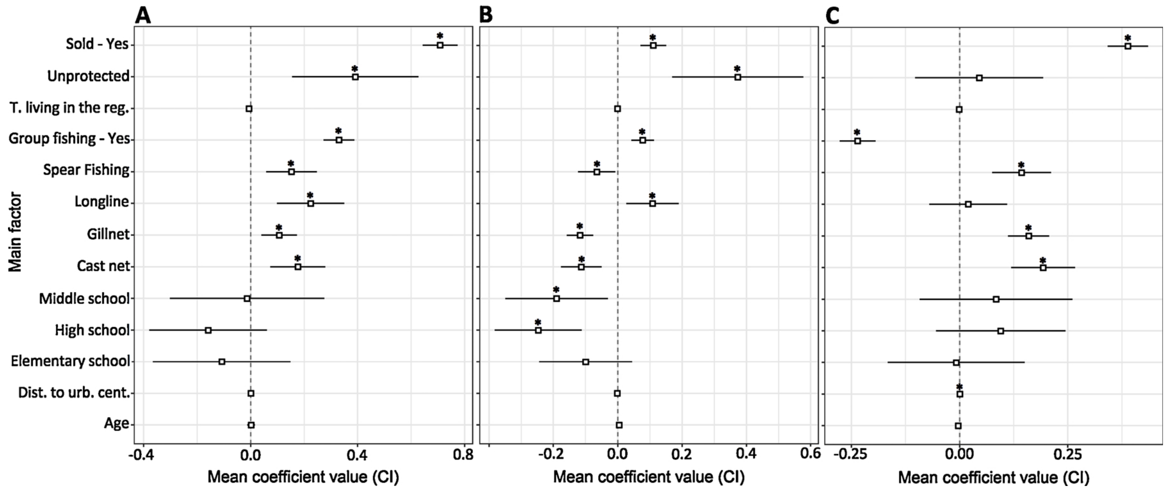

Fig. 1. Coefficient slopes and their respective intervals of confidence (CI) generated by the averaging of mixed models for A) catch (kg), B) effort (hours) and C) catch per unit effort (CPUE). The coefficients associated with levels of categorical variables (fish sales, group fishing, fishing techniques, and education) represent their difference to a fixed baseline level (no sold, protected, no group fishing, angling, and uneducated, respectively). Asterisks indicate coefficient ranges that do not encompass zero and thus show consistent positive or negative influences.

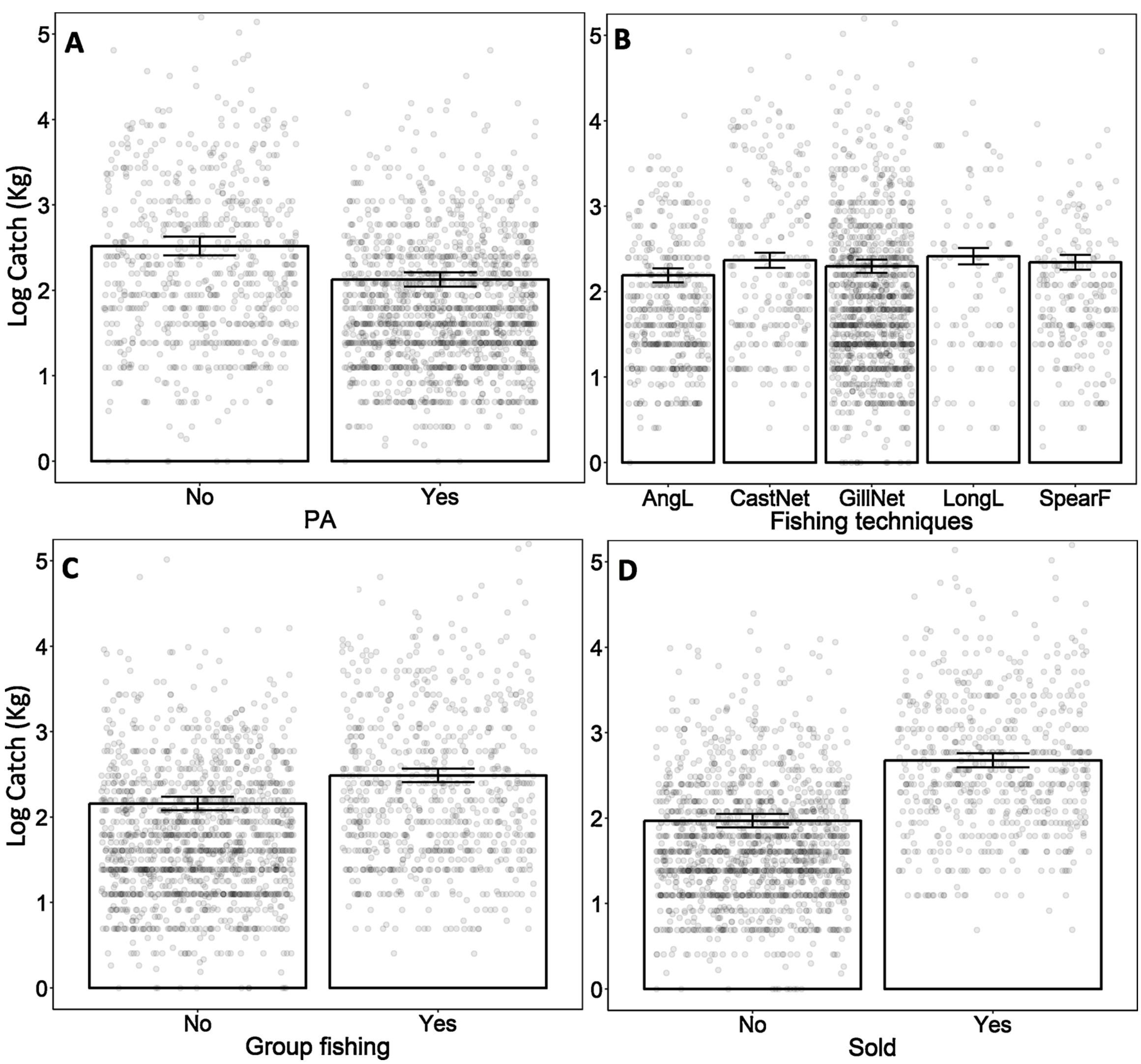

Fig. 2. Marginal effects of A) protected areas (PA), B) fishing techniques, C) group fishing, and D) fish sales on catch based on a model averaging procedure. Error bars represent standard errors. Only significant predictors are presented. Gray dots represent fish landing data.

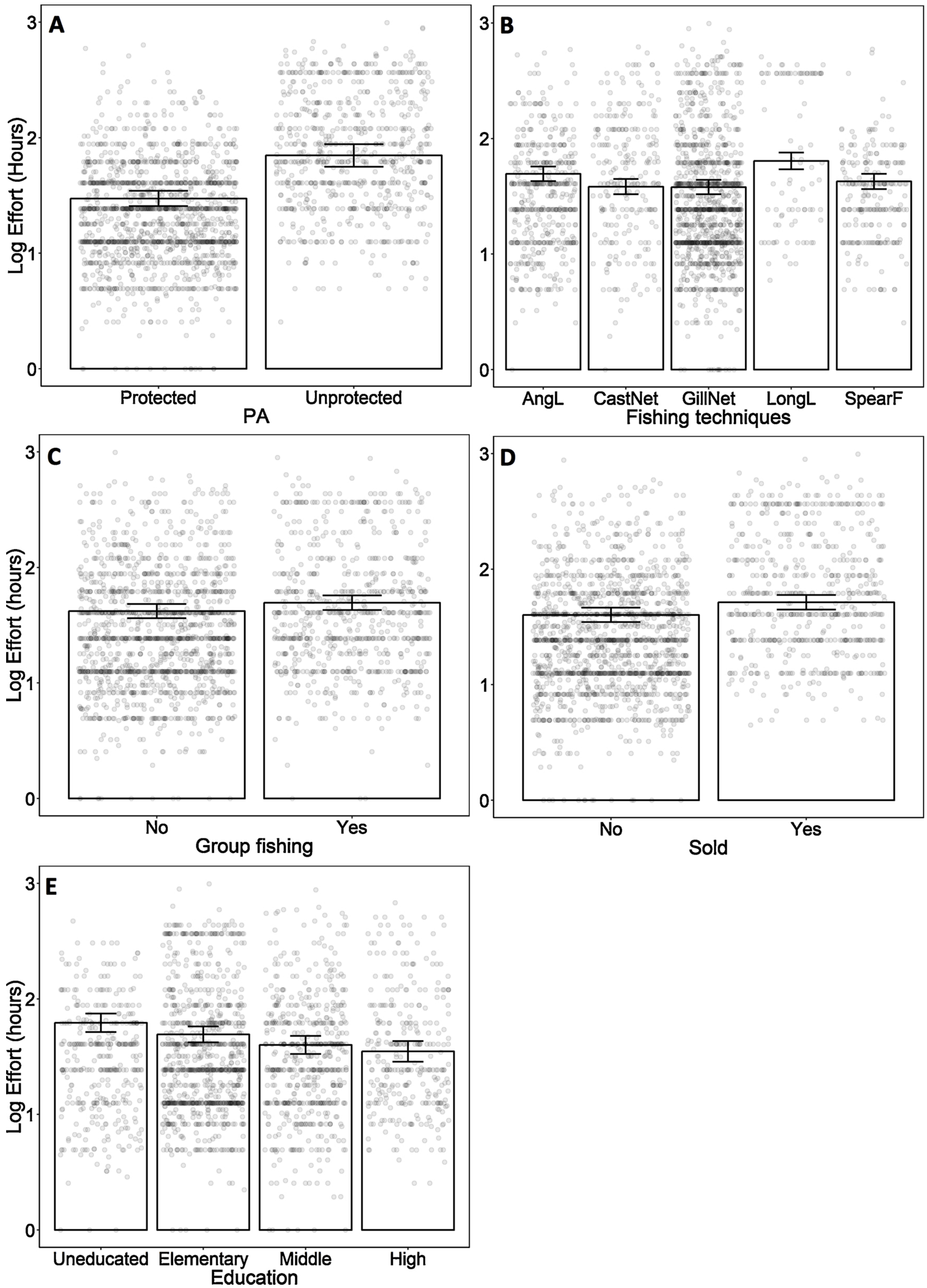

Fig. 3. Marginal effects of protected areas (PA; A), fishing techniques (B), group fishing (C), fish sales (D) and education (E) on fishers' effort based on a model averaging procedure. Error bars represent standard errors. Only significant predictors are presented. Gray dots represent fish landing data.

2011).

At a regional scale, the hypothesis regarding the effects of PA on fish landings was partially confirmed, as our results indicated that PAs can increase CPUE, at least in one of the two studied rivers (Tapajós), besides reducing the fishing effort and hence the risk of overfishing. This difference in the effect of PA on fishers CPUE may be due to differences between these two rivers in terms of remoteness and human establishment. Unprotected areas are less impacted by human settlements and productive activities (agriculture or cattle raising) in the Middle Negro region than in the Lower Tapajós River, as the former region has lower human densities and reduced levels of deforestation (Laurance et al., 2002). Human density in the Amazon basin tends to be associated

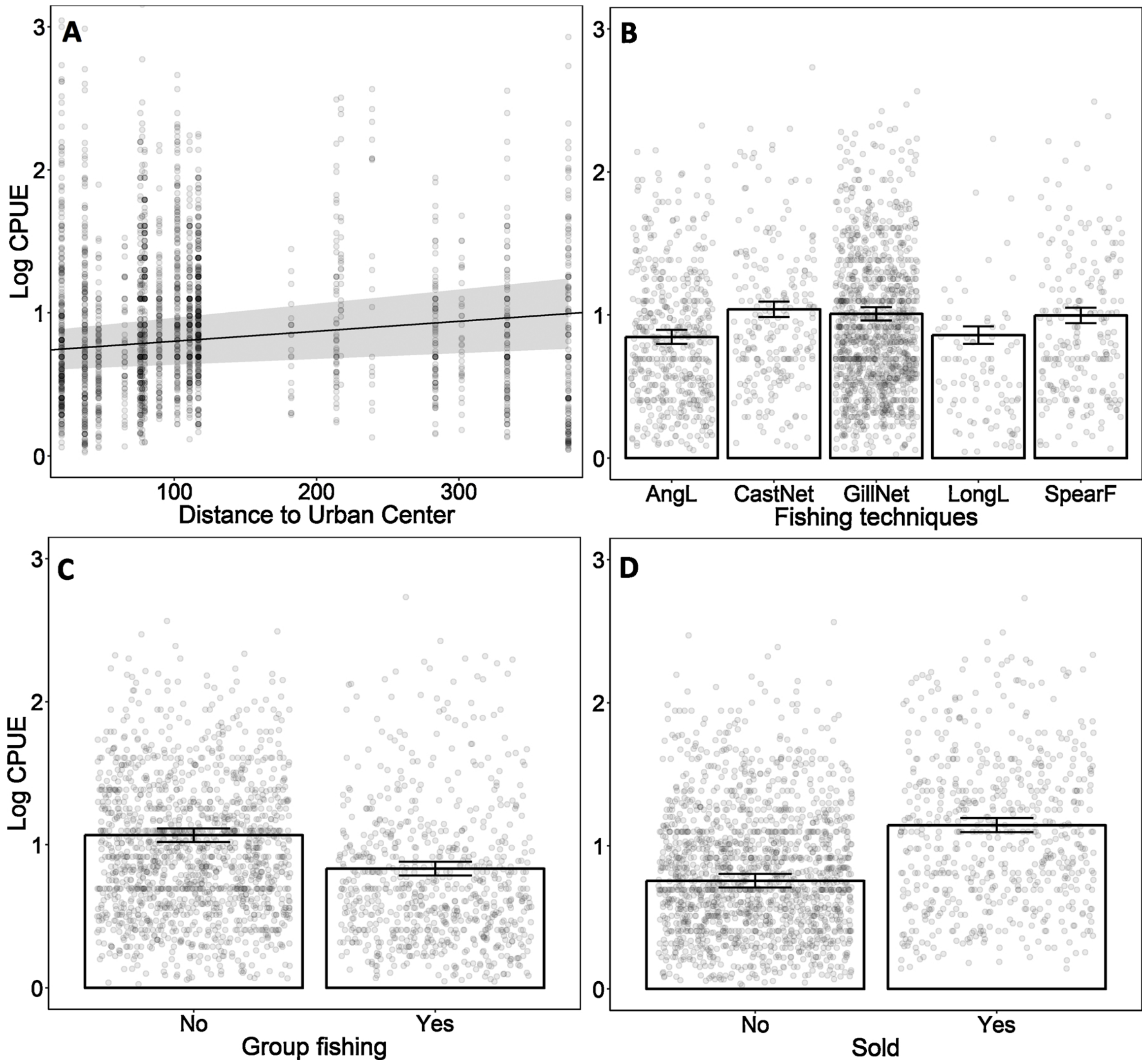

Fig. 4. Marginal effects of distance to the urban center (A), fishing techniques (B), group fishing (C), and fish sales (D) on catch per unit effort (CPUE) based on a model averaging procedure. Error bars represent standard errors. Only significant predictors are presented. Gray dots represent fish landing data.

with a higher demand for resources, including animal protein derived from fish (Bayley and Petrere, 1989; Isaac et al., 2015). Conversely, the forest is positively related to fish abundance and diversity, as floodplain forests provide food and shelter for fish (Arantes et al., 2018). Therefore, the difference in environmental integrity (floodplain forest coverage) and distance to major urban centers (a proxy for human density and demand for fish) among PA and non-PA in the Middle Negro River may be less contrasting than in the Lower Tapajós River. Indeed, a previous study also shows that lakes in Negro River usually have larger fish (individuals and species) than lakes in Tapajós River, which may be partially attributable to an overall better integrity of forests in the former (Keppeler et al., 2018). Although the effect of PA on fish and local fisheries merits more research, our results indicate that PAs which include people within their boundaries (e.g., extractive reserves or sustainable reserves) may benefit freshwater fisheries as already indicated by previous studies (Silvano et al., 2014; Keppeler et al., 2017). Therefore, more effort is warranted to expand PAs in freshwater ecosystems or at least maintain the existing ones, especially those that include local communities in participatory approaches (Lopes et al., 2011). Low compliance, logistical difficulties, short budgets and top-down implementation are among the main problems with PAs in developing countries (Lopes et al., 2013; Alabsi and Komatsu, 2014). A promising alternative is to decentralize decisions and enforcement through co-management systems, which have increased fishing yields in small-scale fisheries, including those in the Brazilian Amazon (Maccord et al., 2007; Castello et al., 2009; Silvano et al., 2014). These co-management arrangements could link individual decision-making with management at broader scales, such as PAs, in a bottom-up framework to improve social equity and sustainable use of resources.

Also at a regional scale, the CPUE of fish landings increased with distance from the urban center, which agreed with our hypothesis, and corroborate a previous study that showed a positive relationship between the distance of urban centers and size of fish sampled in lakes of five Amazonian rivers (Keppeler et al., 2018). This negative effect of the proximity to urban centers on the abundance of fish and on the CPUE of fish landings, may reflect a higher fishing pressure exerted by commercial fisheries and the increased demand for fish near larger cities (Tregidgo et al., 2017; Keppeler et al., 2018). The distance from urban centers and the inaccessibility of aquatic habitats may be relevant for determing the location of new PAs and also contribute to a more effective co-management, increasing fish abundance and CPUE of riverine populations (Silvano et al., 2014). Therefore, distance to urban centers could serve as an indicator of priority areas for conservation and management (Keppeler et al., 2018).

At the individual level, fishing yields and effort were better explained by variables potentially related to optimization behavior of

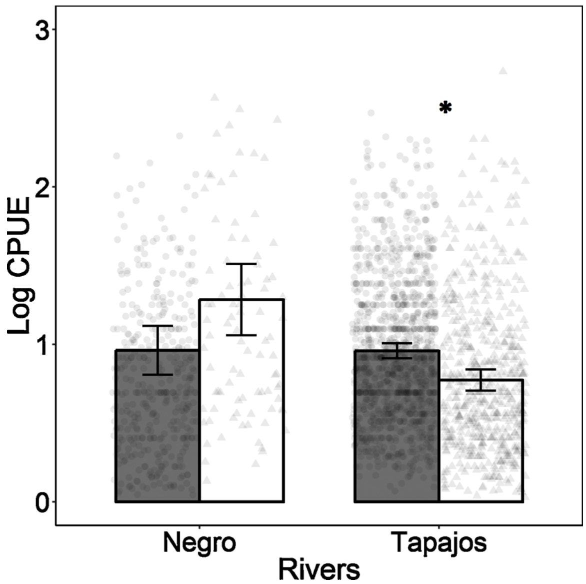

Fig. 5. Marginal effects of protected areas (PA) on the catch per unit effort (CPUE) of fishers from the Tapajós and Negro rivers. Gray bars represent fishers' CPUE within PA and white bars in non-PA. Error bars are SD values. The asterisk indicates significative differences. Gray dots and triangles represent fish landing data collected within and outside PA, respectively.

fishers, while variables related to fishers' local ecological knowledge (LEK; age and time living in the region) were not related to fishing parameters. We considered that formal education and LEK are different forms of knowledge held by fishers: while formal education is provided in schools, LEK is acquired by fishers from their own experiences and from knowledge passed down through generations (Berkes et al., 2000; Johannes et al., 2000; Silvano and Begossi, 2002, 2012). However, the fact that our proxies of fishers' LEK were only weakly associated with fish landings in this study does not mean that these variables and underlying theoretical approaches (LEK) are not relevant to fisheries. Fishers' LEK is an invaluable source of information on fish behavior, ecology, migratory movements and abundance trends over time (Johannes et al., 2000; Silvano and Begossi, 2012), which has also been observed in the Brazilian Amazon (e.g., Nunes et al., 2019; Hallwass et al., 2020; Junior et al., 2020).

Fishers education was the only variable at the individual level associated with fisher experience and knowledge that influenced fishing descriptors. Fishers with lower or no education level tended to spend more time fishing than fishers who had completed middle and high school, but the former did not catch more fish, despite the extra effort. Empirical studies suggest that fishers with low education level may be hesitant to quit fisheries even when it seems economically rational (Panayotou and Panayotou, 1986; Pollnac et al., 2001). If that is the case, fishers with low levels of education may be more strongly affected by changes in fisheries caused by dams or climate change. Conversely, a study conducted in five western Indian Ocean countries suggest that the effect of education on the decision to exit the fisheries or not may be context dependent (Daw et al., 2012). Another possibility would be that fishers with lower educational levels may have more difficulty assessing the cost/benefit ratio of fishing trips and, therefore, they could employ more effort than needed. Regardless of underlying reasons, the observed relationship between educational level and fishing effort suggests to decision makers that increasing access to education in fishing communities can have the additional benefit of reducing fishing pressure (effort), without affecting fishing yields (catch and CPUE). Future

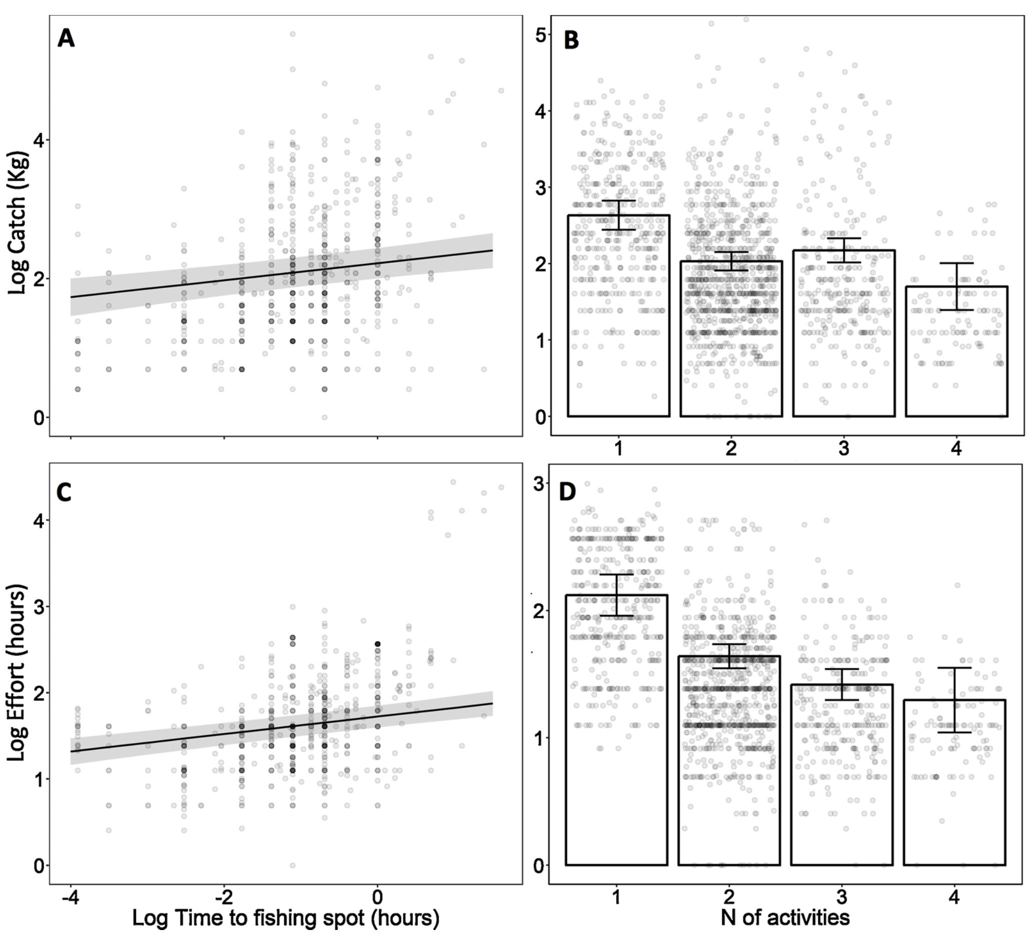

Fig. 6. Marginal effects of time to fishing spot (A-Catch, C-Effort) and number of activities performed (e.g., fishing, farming, rubber tapping, hunting, ecotourism, retail) (B-Catch, D-Effort) on the response variables. These analyses were conducted with a subset of the data and only significant relationships are presented. Gray dots represent fish landing data.

studies could further investigate the interactions between educational level and fishing behavior, but it seems that improved education would provide further benefits to fishing communities.

Fishing technique (gear used) was among the variables that most affected fish catches and effort. Gillnets showed higher catch and CPUE, and less effort, thus being more productive. Gillnets were also the most used fishing gear, as observed in other Amazonian rivers (Bayley and Petrere, 1989; Hallwass and Silvano, 2016; Silvano et al., 2017), which suggests that fishers may be maximizing their catches through the choice of fishing gear, confirming one of the hypothesis from optimal behavior (Table 1). Cast net, spear fishing, and long line were also linked to higher catches, although only the former two gears were also associated to higher CPUE and reduced effort. Nevertheless, even showing a comparable efficiency, cast net and spearfishing techniques were less commonly used than gillnets, possibly because of the required skill and physical effort limit the use of these fishing techniques. Other possibility would be that gillnets could be set and retrieved later, allowing the fishers to engage in other activities, but the presence of aquatic predators (river dolphins, caimans, river otters, among others) may severely limit the amount of time that fishers can be away from their gillnets. These techniques may be also season and habitat specific, as spear fishing should be more effective at lower water levels in flooded forests, as practiced in the Negro River (Begossi et al., 2005). The second most used fishing technique by the studied fishers was angling, which was associated with lower catch and demanded more effort. The observed preference for angling may be due to its higher selectivity (Kenchington, 1993), especially during high water season when fishes are more dispersed and therefore less likely to be caught in gillnets (Hallwass et al., 2013), or due to the fact that hooks and lines are cheaper and easier to repair than most fishing gears.

Contrary to expected (Table 1), fishing in groups increased the catch and the effort (hours) spent fishing, but reduced the individual CPUE. However, optimization theory could still be useful to explain the overall behavior of fishers, as group fishing occurs in less than 30% of the fish landings. Therefore, most fishers work alone most of the time, following the more rewarding strategy. Even considering the lower CPUE, fishing in groups can be an opportunity to strengthen the ties with other members of the community, including kin ties and reciprocity, which are common among fishers (Begossi, 1996).

In those fish landings on which fish were sold, the fishers applied more effort, caught more fish and were more productive (higher CPUE). Although fish sales occurred in less than 27% of the fish landings recorded, sales could be a motivation for some fishers to apply more effort to catch more fish more efficiently. This is also in agreement with optimal foraging models that predict a higher incentive to optimize the catch of more valuable fishing resources (Lopes et al., 2011; Oliveira and Begossi, 2011). On the other hand, even if selling the catch was not the primary goal, those fishers that had higher yields may be more prone to sell the fish caught. The occurrence of fish sales recorded in the fish landings was 77% higher in non-PA than in PA, suggesting an influence of PA restrictions on fishers' behavior, as fish sales are prohibited in two of the studied PA (Extractive Reserve of Negro River and the Tapajós National Forest; ICMBio, 2018).

The fishers who performed more economic activities tended to spend less time fishing and caught less fish as expected. This suggests that the engagement with other activities may attenuate the harvest impacts on fish communities due to a trade-off between time spent on fishing and other activities (turnover effect; Garcia and Cochrane, 2005). Indeed, specialized fishers sold their fish caught on average two and half times more often than fishers with multiple economic activities. These specialized fishers may sell some or all of the fish caught to buy other goods needed, including food from markets (Silva and Begossi, 2009). Amazonian riverine people usually perform multiple activities in mixed economies (McGrath et al., 2008), so those fishers who rely on extra economical activities may go fishing to obtain an additional source of animal protein. Therefore, the diversification of economic activities could be an adaptive strategy for fishers to reduce their dependence on fishing, especially in cases of declining abundance of fishing resources (Huntington et al., 2017). As observed by previous research (Hallwass et al. 2013; Kasperski and Holland, 2013), our results indicate that incentives for economic diversification in riverine communities may reduce fishing pressure and decrease the risks associated with inter-annual variability of fish stocks.

Our results indicate that travel time to a fishing spot was positively related with the catch and fishing effort, but unrelated to CPUE. This agrees with the optimal foraging model from a central place (Table 1), according to which fishers would optimize their catches by compensating longer travels with either higher catches or more intense fishing effort (Oliveira and Begossi, 2011). However, the lack of correlation between CPUE and travel time to fishing spot indicates that higher catches at distant fishing spots do not overcompensate the time expend to reach these areas.

Although drivers at broader spatial scales, such as marine and freshwater PAs, have received more attention in the fisheries literature (Loury et al., 2018), our results highlight the relevance of more subtle drivers operating at the scale of individual fishers, which could be addressed by theoretical frameworks related to individual behavior, such as optimal foraging models (Aswani, 1998). These results contribute to improving the understanding of fisheries performance in complex socio-ecological systems, such as the two Amazonian rivers studied, which have a high fish diversity and ongoing conservation initiatives (Goulding et al., 1988; Keppeler et al., 2018), but may be adversely affected by future development projects, such as dams (Winemiller et al., 2016). A better understanding of the relative importance of drivers influencing fisheries outcomes could also help to devise more effective management interventions to ensure the food security in highly variable, unpredictable and poorly studied tropical small-scale fisheries (Lynch et al., 2017; Fluet-Chouinard et al., 2018).

Credit author statement

FWK, GH, FS and RAMS designed the study; RAMS, GH, FS, and LHTS collected and curated the data; FWK and FS analyzed the data; FWK wrote the first draft of the manuscript; All authors reviewed and contributed to the final version of the manuscript

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.fishres.2020.105571.

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