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Influência de áreas protegidas e da variação ambiental na assembléia de
peixes em um rio de água clara na Amazônia

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Influência de áreas protegidas e da variação ambiental na assembleia de peixes em um rio de água clara na Amazônia

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RESUMO

Unidades de conservação (UC) tem sido a principal estratégia para conservação biológica ao longo de todo o planeta. Entretanto, nos últimos anos as UC tem sido desacreditadas, diminuídas e desoficializadas. Neste estudo, o papel das UC em relação a proteção da fauna ictica da pesca é investigada no Rio Tapajós. Parâmetros ambientais foram quantificados para distinguir entre as influências relativas dessas variáveis e da pressão pesca. Três hipóteses foram testadas: 1) UC sofrem menor pressão de pesca do que áreas não protegidas; 2) Pescadores de UC têm captura por unidade de esforço (CPUE) de peixes maior que os pescadores de áreas desprotegidas; 3) Assembléia de peixes de lagos de planície de inundação localizados em áreas não protegidas tem menor biomassa, abundância, presença de peixes de interesse, riqueza, tamanho médio e nível trófico do que lagos localizados em UC. Doze comunidades ribeirinhas de duas UCs de uso sustentável e uma área não protegida foram amostradas. A pressão pesqueira de cada área foi estimada usando o registro de 2013 desembarques pesqueiros de 51 pescadores durante 12 meses. Além disso, duas coletas (período de águas altas e baixas) foram realizadas em 4 lagos em cada uma das áreas para amostrar a assembléia de peixes e 11 variáveis ambientais ligadas a físico-química da água, estrutura e morfologia dos lagos. O CPUE dos pescadores foi menor na área não protegida do que nas UCs e a biomassa total de peixes capturados foi maior na área não protegida. Estes resultados são a primeira evidência que UCs voltadas principalmente para conservação terrestre (florestal) podem atuar sinergicamente para reduzir os níveis da pesca e aumentar a densidade de peixes alvo na bacia amazônica. Por outro lado, diferenças consistentes nos descritores biológicos entre as UCs e a área protegida não foram encontrados nos lagos de planície de inundação. Este resultado é corroborado quando os desembarques pesqueiros oriundos dos lagos são analisados separadamente, os quais mostram valores de CPUE de pescadores similares entre as UCs (áreas protegidas) e a área desprotegida. Estes descritores biológicos estiveram mais relacionados com parâmetros ambientais, como profundidade, cobertura de habitat e tamanho e morfologia dos lagos. Diferença na pressão pesqueira entre os lagos e o rio e também relacionadas ao co-manejo local podem estar influenciando a ausência de relação entre a assembleia de peixe de lagos e as UCs. Os resultados obtidos nesse trabalho indicam que a variação ambiental entre os lagos cria diferentes associações de espécies de peixe no espaço e no tempo e portanto essas variáveis devem ser levadas em conta em qualquer plano de manejo na Amazônia.

Palavras-chave: pesca de pequena escala, conservação, heterogeneidade espacial, Rio Tapajós, manejo pesqueiro, impactos ambientais

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INTRODUÇÃO GERAL

O estabelecimento de unidades de conservação (UC) tem sido a principal forma utilizada para a preservação da biodiversidade a nível global (Mascia et al., 2014). Desde a primeira UC, criada em 1872 em Yellowstone, o número de áreas protegidas tem aumentado exponencialmente (Andrade and Rhodes, 2012). Atualmente, existem mais de 144 mil UCs espalhadas por todo o mundo, cobrindo uma área de aproximadamente 19 milhões de km², ou 12,9% da superfície da terra (Chape et al., 2008). Entretanto, a baixa fiscalização somado a um manejo inadequado tem levado a maior parte das UCs a apresentarem resultados insatisfatórios quanto as questões sócio-ambientais (Leverington et al., 2010). Ironicamente, esta incapacidade de atingir os objetivos traçados tem sido utilizada como um argumento para a desoficialização e diminuição de UCs em todo o planeta (Mascia and Pailler 2011; Ferreira et al, 2014; Mascia et al, 2014).

Ambientes de água doce estão entre os ecossistemas mais ameaçados no planeta (Saunders et al., 2002; Abell et al., 2008). Estimativas apontam que a taxa de extinção de organismos de água doce será até cinco vezes superior do que o encontrado para organismos terrestres (Ricciardi et al., 1999). Isso se aplica especialmente a peixes, que são considerados o táxon mais ameaçado do mundo entre os organismos de grande porte (Carrizo et al., 2013). Apesar dos ecossistemas aquáticos de água doce perfazerem menos de 0,3% de toda a água presente na superfície terrestre, estes abrigam mais de 15 mil espécies de peixes, o que representa 53% de todos os peixes e 25% de todos os vertebrados (Reid, 2013). Existem algumas evidências suportando o efeito positivo de UC sobre atributos biológicos de assembleias de peixes (Ex: Biomassa, tamanho médio, diversidade, densidade) em ecossistemas marinhos (Halpern, 2003; Roberts et al., 2005). Entretanto, o mesmo não pode se dizer para ecossistemas de água doce, cujos efeitos são muito pouco documentados e explorados (Nel et al., 2007; Gaston et al., 2008; Abraham and Kelkar, 2012). Além disso, UCs que incluem ecossistemas de água doce são quase sempre projetadas com o objetivo de proteger os ambientes terrestres (Rodríguez-Olarte et al., 2011). Como consequência, a maior parte das UCs incluem apenas alguns fragmentos de bacias hidrográficas ou riachos, deixando de incluir regiões essenciais para o funcionamento dos ecossistemas, e, conseqüentemente, tornando-as incapazes de mitigar impactos antropogênicos (Ex: Eutrofização e

contaminação por mercúrio de áreas mais a montante) e conservar a biodiversidade de peixes (Suski and Cooke, 2007; Rodríguez–Olarte et al., 2011).

. Os peixes formam hotspots de diversidade e são responsáveis por muitos processos funcionais dentro dos ecossistemas aquáticos de água doce (Vanni, 2002; Taylor et al., 2006; Horn et al., 2011), além de servirem como base alimentar e de sustento para milhões de pessoas em todo o planeta. Segundo a FAO (2014), pelo menos 21 milhões de pessoas trabalham exclusivamente com a pesca em ambientes aquáticos continentais. Infelizmente, a maximização dos lucros em um curto prazo, levou a indústria da pesca a uma crise. Declínio de peixes tem ocorrido em todo mundo desde os anos 80 (Pauly et al., 2002). De forma similar, a composição de espécies presentes nos desembarques pesqueiros também vem apresentando mudanças. Em vários lugares observa-se a substituição de grandes peixes predadores por pequenos peixes planctívoros e invertívoros, gerando um efeito de redução do comprimento das cadeias alimentares (Pauly et al., 1998). Os peixes de vida longa, maturação tardia e de maior tamanho são afetados mais adversamente pela pesca do que aqueles peixes de vida curta, rápida maturação e menor tamanho corporal (Winemiller, 2005). A pesca seletiva unidirecional também influencia as assembléias de peixes através da redução do tamanho médio, idade e tamanho da primeira maturação (Rochet, 1998). Assim, uma alta pressão pesqueira pode alterar a estrutura das cadeias alimentares e, em uma escala mais ampla, afetar o fluxo de matéria e energia dos ecossistemas (Andersen e Pedersen, 2010).

Na maior parte das regiões do planeta, os principais impactos sobre a pesca em água doce não são causados por sobre-exploração, mas sim por fatores externos a pesca, como hidrelétricas e a poluição dos corpos aquáticos (Arlinghaus et al., 2002). Entretanto, essas conclusões devem ser analisadas com cuidado, já que a maior parte das pescas interiores, especialmente aquelas feitas em países tropicais subdesenvolvidos, são de pequena escala e descentralizadas, o que dificulta a fiscalização e observação dos impactos (Allan et al., 2005; Chuenpagdee and Pauly, 2008; Castello et al., 2013a). Além disso, em muitos casos, a pesca de pequena escala é reconhecida por poder levar os estoques pesqueiros locais ao colapso, devido a uma incompatibilidade entre leis governamentais e particularidades locais (Berkes et al., 2001; Prince, 2003; Castello et al., 2013a). Por essa razão, alguns estudos sugerem que a pesca de pequena escala em paisagens heterogêneas deveria ser manejada em uma

escala mais local em vez de ser regulado por regras gerais de manejo, como o ditado por UC e leis governamentais (Berkes et al., 2001; Prince, 2003; Castello et al., 2013a).

Na Amazônia, a maior bacia hidrográfica do planeta (Goulding et al., 2003), a pesca é considerada uma das principais forças antropogênicas influenciando a assembleia de peixes (Santos and Santos, 2005; Castello et al., 2013b). Atualmente, cerca de 43,9 % da Amazônia Brasileira (2,2 milhões de km²) estão sob proteção ambiental na forma de UC, nas categorias de proteção integral, uso sustentável e terras indígenas (Veríssimo et al., 2011). Excluindo-se as áreas indígenas, o número de áreas protegidas cai para 26,5% (1,11 milhões de km²), o que ainda é superior ao encontrado nos biomas brasileiros da Caatinga (7,5%), Cerrado (8,2%), Mata Atlântica (9,7%) e Pampa (3,3%) (MMA, 2012). Entretanto, mesmo com o extenso território sob a proteção de UC, existem sinais de sobrepesca de algumas populações de peixes comerciais na Amazônia (Petreire et al., 2004; Arantes et al., 2005; Castello et al., 2013b). A principal espécie de peixe explorada no início do século XX (*Arapaima gigas* – pirarucu) é agora considerada ameaçada, enquanto que dentre as 18 espécies que dominam o mercado pesqueiro atual, uma é considerada ameaçada e outras quatro são consideradas sobre-explotadas em pelo menos uma região da Amazônia (Castello et al., 2013b). Nesse sentido, a eficiência das UCs para proteger os estoques pesqueiros da sobrepesca é dúvida. Alguns estudos sugerem que o aplicação e fiscalização das leis raramente existe na Amazônia, dificultando o controle da sobre-explotação de peixes (Castello et al., 2013). Entretanto, pelo nosso conhecimento, nenhum estudo comparou a integridade da assembleia de peixes e a intensidade da pesca entre UC e áreas não protegidas na Amazônia.

A presente dissertação tem por objetivo investigar a intensidade da pesca em pequena escala e seu impacto sobre as assembleias de peixes entre duas UCs de uso sustentável e uma área desprotegida, sem qualquer gestão específica. Os estudos foram realizados na área de planície de inundação do rio Tapajós, afluente de águas clara do rio Amazonas. Como a planície de inundação Amazônica apresenta uma paisagem profundamente heterogênea (Junk et al., 1989), uma série de variáveis ambientais relacionadas com a estrutura do habitat, morfologia e parâmetros físico-químicos da água foram medidos para distinguir a influência dessas variáveis e a pressão pesqueira. Três hipóteses foram testadas: 1) As duas UCs sofrem menos pressão de pesca (biomassa de peixes capturados) do que a área não protegida; 2) Pescadores de UC têm captura por unidade de esforço (CPUE) de peixes maior que os pescadores de áreas

desprotegidas; 3) As assembleias de peixes de lagos de planície de inundação localizados em áreas não protegidas tem menor biomassa, abundância, presença de peixes de interesse, riqueza, tamanho médio e nível trófico do que lagos localizados em UC.

ARTIGO¹

Influence of conservation units and environmental heterogeneity on lake fish assemblages and small-scale fisheries in a tropical clear water river in the Brazilian Amazon.

Friedrich Wolfgang Keppeler, Gustavo Hallwass and Renato Azevedo Matias Silvano²

Abstract

Conservation units (CU) have been the main strategy to biological conservation worldwide. However, in the last years CUs have been discredited and, consequently, many of them have been downsized and degazetted. In this study, the role of CU regarding the protection of fish fauna from fisheries was investigated in the Tapajós River, a clear water tributary of the Amazon River. Environmental parameters were quantified to distinguish between the relative influences of these variables and fishing pressure. Three hypotheses were tested: 1) The CUs experience lower fishing pressure than the unprotected area; 2) Fishermen from CUs have catch per unit effort (CPUE) of fish biomass higher than fishermen from unprotected areas; 3) Fish assemblages from the unprotected area have less total biomass, abundance, presence of target fish and richness and lower mean body size and mean trophic level than those from CUs. Twelve riverine communities from two CUs of sustainable use and an unprotected area were sampled. The fishing pressure of each area was estimated through the record of 2,013 fish landings from 51 fishermen during twelve months. Besides, two surveys (high and low water season) were undertaken in four lakes of each area to sample fish assemblages and 11 environmental variables related to physical-chemical parameters of water and lakes' structure and morphology. Overall, the CPUE of fishermen was lower in unprotected areas than in the CUs and the total fish biomass caught was higher in unprotected areas. These results are the first evidence that the conditions provided by CUs act synergistically to reduce the levels of fishing and increase the density of target fish in the Amazon Basin, reinforcing the importance of these protected areas to socio-ecological purposes. On the other hand, consistent differences were not found in the biological descriptors of fish assemblages between CUs and unprotected areas in the

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floodplain lakes. This result is corroborated when the fish landings originated from lakes were analysed separately, showing similar CPUE values between protected and unprotected areas. These biological descriptors were more related with environmental parameters, such as depth, habitat coverage and lakes' morphology and size. Differences on fishing pressure between lakes-main river and also the local management may lead the absence of relationship between fish assemblage in lakes and CUs. Anyhow, the environmental variation between floodplain lakes create different association of fish species and therefore these variables must be considered in management or conservation programs.

Key words: small-scale fisheries, conservation, spatial heterogeneity, Tapajós River, fisheries management, environmental impacts

1. Introduction

Conservation units (CU) have been the main strategy to conserve species, habitats, and associated ecosystem services worldwide (Mascia et al., 2014). Since the first CU, created in Yellowstone in 1872, the number of new area designated to biological conservation have increased exponentially (Andrade and Rhodes, 2012). Currently, there are more than 144 thousands of CUs spread throughout the world, covering an approximate area of 19 million km², or 12.9 % of earth's surface (Chape et al., 2008). However, the inadequate management and poorly surveillance of most CUs ultimately lead to poor conservation standards (Leverington et al., 2010). Furthermore, the imposition of laws in a top-down fashion lead to conflict with local people, whose history and culture are often overlooked (Andrade and Rhodes, 2012). Ironically, the failure to achieve environmental and social objectives are being used as arguments to a new worldwide trend of downsizing and degazetting the current CUs to allow commercial exploration of natural resources (Mascia and Pailler 2010; Ferreira et al., 2014; Mascia et al., 2014).

Freshwater ecosystems are among the most threatened systems in the world due to human activity (Saunders et al., 2002; Abell et al., 2008). Hence, the extinct rate for freshwater organisms is estimated to be up to five times higher than for terrestrial organisms (Ricciardi et al., 1999). This is particularly true for fishes, which has high levels of endemism and form hotspots of diversity in freshwaters (Rosenfeld 2002). Although freshwater ecosystems encompass 0.3 % of all surface water present on Earth, these

ecosystems are habitat for more than 15 thousand of fish species, representing 53% of all fish in the world and 25% of all vertebrates (Reid, 2013). There are several evidences supporting the positive effects of CUs on some biological attributes of fish assemblages (eg. biomass, mean size, diversity, density) in marine ecosystems (Halpern, 2003; Roberts et al., 2005). On the other hand, the effects of CUs in freshwater ecosystems are still poorly documented (Nel et al., 2007; Gaston et al., 2008; Abraham and Kelkar, 2012). Most CUs that include freshwater ecosystems have been designed to protect terrestrial ecosystems in the first place (Rodríguez–Olarate et al., 2011). As a consequence, most CUs include just some fragments of watersheds or streams, thus failing to include essential regions for ecosystem function, mitigation of anthropogenic impacts (eg. eutrophication and mercury contamination from upstream), and maintenance of fish biodiversity (Suski and Cooke, 2007; Rodríguez–Olarate et al., 2011).

Besides being a diverse and abundant group of organisms that play key roles in the functioning of aquatic ecosystems (Vanni, 2002; Taylor et al., 2006; Horn et al., 2011), fish are a vital food source for millions of people worldwide (FAO, 2014). Unfortunately, the maximization of earnings in a short-term instead of a sustainable and profit harvesting in a medium/long-term led the fishing industry to a crisis. Fish declines have been occurring worldwide since the 80s (Pauly et al., 2002), and the composition of landings have been changing, as large predatory fish have been replaced by small planktivorous and invertivorous fish (fishing-down process) in many harvested ecosystems (Pauly et al., 1998). Long-lived fish, which have late maturation and bigger size, are more adversely affected by fisheries than those fish with short life, fast maturation and smaller body size (Winemiller, 2005). The current size-selective fishing also induce demographic changes in fish populations, such as the decrease of mean size and the age of first maturation (Rochet, 1998). Thus, a high fishing pressure may alters the structure of food webs and, in a broader scale, the flux of material and energy of ecosystems (Andersen and Pedersen, 2010).

According to Arlinghaus et al. (2002), in most regions of the world, the main impacts over freshwater fisheries were not caused by overharvesting, but by factors not related to fisheries, such as impoundments and pollution of rivers. However, this conclusion must be viewed cautiously, since most freshwater fisheries, especially in tropical developing countries, are small-scale and decentralized, difficulting the recording of fish landings and the estimation of impacts (Allan et al., 2005; Chuenpagdee and Pauly, 2008; Castello et al., 2013a). Small-scale fisheries may drive local fish stock to collapse due to the incompatibility between governmental laws and local particularities (Berkes et

al., 2001; Prince, 2003; Castello et al., 2013a). Indeed, some studies suggest that small-scale fisheries in heterogeneous landscapes should be managed in a local scale, instead of being regulated by general management rules of CUs and governmental laws (Berkes et al., 2001; Prince, 2003; Castello et al., 2013a).

The Amazon is the biggest freshwater basin in the world (Goulding et al., 2003), where fishing is considered to be one of the main anthropogenic forces influencing fish assemblages (Santos and Santos, 2005; Castello et al., 2013b). Nearly 2.2 million km² (43.9%) are inside CU (integral protection, sustainable use and indigenous lands) in the Brazilian Amazon (Veríssimo et al., 2011). Nevertheless, the intense fishing in the basin led one species to the threatened status and there are evidences of overexploitation for other four species (Castello et al., 2013b). Besides, Castello et al. (2011) observed a current fishing-down process in five of nine most-caught fish in the Lower Amazon region. Therefore, the efficiency of CU to protect fish stock from overharvesting is uncertain. Several studies suggest that the enforcement and implementation of laws hardly exist in the Amazon, making it difficult to control overexploitation of fish (Castello et al., 2013a, b). Floodplain lakes are among the most important and productive environment for fisheries along floodplains of high order rivers in the Amazon basin (MacCord et al., 2007; Silvano et al., 2009; Hallwass et al., 2013). In a regional and local level, studies have shown higher abundance of commercial fishes in floodplain lakes where fishing is banned or restricted by local fishers according to co-management in the Brazilian Amazon (Almeida et al. 2009, Silvano et al. 2009, 2014). However, to our knowledge, no study has compared the integrity of fish assemblages and the intensity of fisheries between protected (CU) and unprotected areas in the Brazilian Amazon.

The objective of this study was to compare the fishing pressure of small-scale fishery and its impact over fish assemblages between two distinct CUs of sustainable use and an unprotected area without any specific management in the floodplain area (main river channel and lateral lakes associated) of Tapajós River, a large clear water river in the Brazilian Amazon. Three hypotheses were tested: 1) The two CUs experience lower fishing pressure (fish biomass caught) than the unprotected area; 2) Fishermen from the two CUs have a higher catch per unit effort (CPUE) of fish biomass than fishermen from unprotected area; 3) Fish assemblages from lakes in the unprotected area have lower total biomass, abundance, presence of target fish, richness, mean body size and mean trophic level than fish assemblages in the CUs. As floodplain lateral lakes are heterogeneous entities (Junk et al., 1989), several environmental variables, related to habitat structure, morphology and

water physical-chemical parameters were measured to distinguish between the relative influences of environmental variation and fishing pressure.

2. Material and Methods

2.1. Study area

The studied area are located in the lower section of Tapajós River, between the coordinates 2° 45'00" S - 3° 25'00" S e 55° 19'00" W – 54°59'00" W (Fig. 1). The water of the Tapajós River is considered to be of the clear water type, which is oligotrophic with low levels of sediment and nutrient concentration (Goulding et al., 2003). This river is situated in the Amazon Basin, where the climate is tropical humid with mean temperatures of 25.5°C and annual variation lower than 5°C (IBAMA, 2004). In the lower section of Tapajós River, the annual mean precipitation is 1820 mm with high seasonal variation (abundant rains in January-March). Consequently, the water level of the river varies significantly throughout the year. The peak of water level occurs in May-June and then decline until November-December, when the lower water levels are found (ANA, 2012). The distance between the opposite margins in the lower section of Tapajós River is large, reaching more than 15 km in some areas.

There are two CUs of sustainable use (Fig. 1) in the lower section of Tapajós River: The National Forest of Tapajós (FLONA) and The Extractivist Reserve of Tapajós-Arapiuns (RESEX). The FLONA was created in 1974 through the federal decree N° 73.684 (IBAMA, 2004). Initially, this CU had had the only objective of sustainable use of timber and only in 1992 it began a process for fauna protection as well. On the other hand, the RESEX was officialy created in 1998, after almost 20 years of a popular struggle against illegal logging (ICMBIO, 2008). The riverine population of both units rely their activities on a diversified system of subsistence, including small scale agriculture, extrativist forest production, livestock farming (mainly chickens), fishing and hunting (IBAMA 2004; ICMBIO 2008). In relation to fisheries, both CUs only allow artisanal fishing gear, such as longlines, gillnets, hand lines and harpoons. The RESEX allows selling the fish, while in FLONA the commerce of fish is not accepted. Besides, the comercial fishing of large scale, typically from big cities, is not allowed in the main channel of Tapajós River between both CUs. On the other hand, the area outside from both CUs has a human density 10 times higher and both the commercial and artisanal fisheries are common. In 2003, two CUs from the category of Environmental Protected Area (EPA or

APA in Portuguese) were established in the area outside from FLONA and RESEX. In this study, these areas were considered as unprotected, because these EPAs are young and the management rules are not grounded. An official document was written for these areas in 2012, which contain some guidelines for fisheries (eg. size of gillnets), however none management plan was created so far. Besides, the APAs do not have buffer zones, which prevents the fishing control in the main channel of Tapajós River.

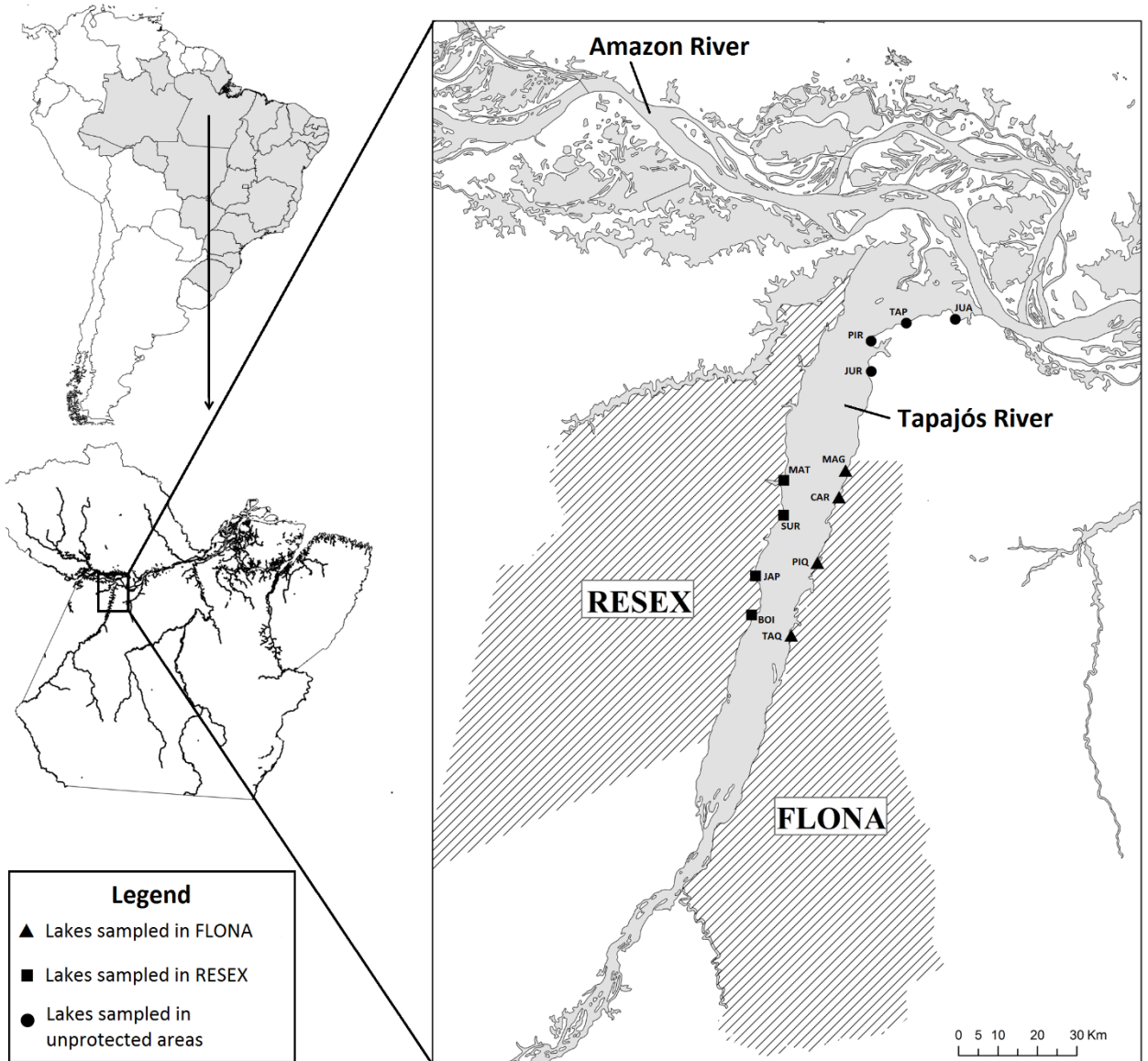


Fig. 1. Location of the study area in the Tapajós River (Brazilian Amazon). The twelve floodplain lakes, where the fish samples was conducted, are shown. Each lake is associated with a code (eg. TAQ), which can be consulted in table 1 for more specific details.

2.2. Selection of sampled lakes and riverine fishing communities

Four riverine communities were selected in each of the three studied regions (FLONA, RESEX and unprotected area; Fig. 1) following two basic premises: i- Minimum distance of 10 km between each riverine community; ii- Fishers of the riverine community accepted to participate in the study. The riverine communities selected in this study are similar to the other ones present in the region, which are generally composed by a small number of families (Mean=47.17, SD=42.63; Table 1; IBAMA, 2004; ICMBIO, 2008) of mixed origin (indigenous, black and caucasian), low educational level and low mean wage. After the selection, the leader of each community was asked to indicate the lake most exploited by fishers. These lakes were selected for further analysis of fish assemblages (see below).

2.3. Measure of fishing pressure

The fishing landings of the riverine communities were measured during 12 months to estimate fishing pressure in each region. The monitoring of fish landings was conducted through a participatory method. Fishermen of each riverine community were selected to record their own fish landings through the following criteria: i) To have interest to participate in the study; ii) To have at least five years of basic study; iii) To fish at least 3 days in the week. The fishermen that fulfilled the criteria above received a set of materials (pencil, eraser, watch, forms, briefcase and weighing device) required to record their landings. Each fisherman was trained individually and requested to registrate the five first fish landings of each month, beginning in August 2013 until July 2014. Fishermen were requested to record the composition of catch (kind of fish caught), catch weight, fishing site (lake or river), the time spent and the number of fishermen in each fishery. Besides, every 15 days phone calls were made to the fishermen to discuss and solve any doubt regarding data recording. The filled forms of fish landings were collected every three months. Although 78 fishermen started to recording their fishing landings in the beginning of the study, 51 participated in the whole study, which amounted to a total of 2,013 fish landings recorded (Table 1). Unfortunately, all fishermen from Maracanã community (near Juá lake; fig. 1), located in the unprotected area, did quit the study. Therefore, we estimated fishing pressure in the unprotected area using data from three riverine communities (Fig. 1; Table 1).

2.4. Fish sampling and biological measures

We conducted fish samples in floodplain lakes, because they are important habitats to support small-scale fisheries in both white and clear water rivers in the Brazilian Amazon, besides being suitable spatial units for sampling and management, as lakes have clear defined boundaries during the low water period (Silvano et al. 2009, 2014). Two samplings were undertaken in each one of the 12 lakes indicated by the leaders of riverine communities (Fig. 1, Table 1). The first sampling was made in July (high water season) and the second was made in November (low water season). Fish were collected using two sets of gillnets (~420 m² each) with different mesh sizes (15, 25, 35, 50, 60, 70 and 80 mm between opposite knots) during ~ 9:30 hours (SD=0:46), starting around 8:30 a.m and ending around 6:00 p.m. The gillnets were checked every 2 hours and the fish trapped in the net were collected. Gillnets were used to sample fish in this study because it is the main type of fishing method used by fishermen in Amazon (MacCord et al., 2007; Hallwass et al., 2013), besides being widely used in scientific studies related to fisheries.

Table 1

Number of fishermen who participated throughout the study and the number of fish landings recorded in the studied riverine communities. The number of families in each community is shown. The associated lakes were indicated by the community leader as being fishing spots. In these lakes we conducted the samples of fish assemblages. The location of each lake are in the Fig. 1 according to its code.

Regions	Riverine community	Number of families in each riverine community	Associated lake	Number of Fishermen who participated in the study	Number of Fish Landings
FLONA	Maguari	82	Maguari (MAG)	3	68
	Acaratinga	20	Caranazal (CAR)	4	161
	Piquiatuba	86	Piquiatuba (PIQ)	5	209
	Pini	32	Taquara (TAQ)	8	367
RESEX	Boim	92	Boim (BOI)	6	199
	Jauarituba	52	Japequara (JAP)	4	173
	Surucuá	95	Grande (GRA)	4	200
	Vila do Amorim	102	Mato (MAT)	5	121
Unprotected area	Pindobal	37	Jurucurí (JUR)	3	143
	Alter do Chão	>102	Piranha (PIR)	4	189
	Ponta de Pedra	56	Taquara (TAQ)	5	183
	Maracanã	>102	Juá (JUA)	-	-
Total				51	2013

Each individual fish captured was measured to standard length (SL, precision to 0.1 cm), weighed (to precision of 1 g), anaesthetized with clove oil, preserved in a 10% formalin solution and identified to species level. When many individuals of the same species in a given sample were caught, a subsample was collected for species identification (typically 10 or less individuals, due to logistical constraints) and the remaining fish were identified in the field and donated to local people. More details of these sampling procedures can be found in previous studies (Silvano et al., 2009, 2014).

The sampled fish were also desiccated for diet analysis in order to estimate trophic position. Ingested prey was identified to the lowest taxonomic level possible (generally family or order) using specialized literature (Merritt and Cummins, 1996; Fernandez and Dominguez 2001; Hamada et al., 2012; Queiroz et al., 2014). The volumetric method (Herran, 1998) was used to quantify prey importance. Additional diet information were also included from literature for those species with less than 10 individuals analyzed (Mérona et al., 2001; González and Vispo, 2003; Melo et al., 2004; Mérona and Rankin-de-Mérona, 2004; Layman et al., 2005; Blanco-Parra and Bejarano-Rodríguez, 2006; Silva, 2006; Freitas, 2007; Godoi, 2008; Silva et al., 2008a; Silva et al., 2008b; Vasconcelos and Oliveira, 2011; Hawlitschek et al., 2013; Sá-Oliveira et al., 2014; Details in supplementary data - A). In cases when few or none individuals were dissected in this study and none specific literature information were available for a given fish species, the trophic level of this species was estimated based on close related species from the same genus.

2.5. Characterization of lake structure, morphology and physical-chemical parameters

Variables related to physical-chemical parameters of water (pH, conductivity, temperature, depth and euphotic zone), the habitat coverage (percentage of macrophytes, flooded forest and pelagic zone), the morphology (surface area and shoreline development) and the distance to the Amazon River for each lake and for each season were measured. These variables were chosen due to their reported influence on fish assemblages in previous studies (Junk et al., 1983; Rodriguez and Lewis, 1997; Tejerina- Garro et al., 1998; Olden et al., 2001; Petry et al., 2003; Carolsfeld et al., 2004).

Twelve measures of physical-chemical parameters of water (six measures between 9-10 a.m. and six between 3-4 p.m.) and depth were made for each lake and for each season. The pH, conductivity and temperature were measured using a Digital Water Quality Checker, whereas the euphotic zone was estimated through a Secchi Disk. The depth was measured using a graduated cord. The percentage of habitat coverage was estimated

visually by a single person. Since the sizes of most lakes were not large enough to be precisely measured by satellite images, the visual method turned out to be more accurate to measure habitat coverage.

The surface area, shoreline development and the distance to Amazon River were estimated using images from the Landsat5 satellite, obtained through the National Institute for Space Research (INPE, 2014). The shoreline development was calculated through the following equation:

$$\text{Shoreline development} = \frac{L}{2\sqrt{\pi * S}}$$

, where L is the shoreline length and S is the surface area of the lake. Due to the absence of sharp images (without clouds) during the study year, images from the same season of the study but from different years were used: Low water season (November) of 2008 and High water season (July) of 2009. According to records of water levels of Tapajós River obtained from the Hydrological Information System of Brazil (HidroWeb; ANA, 2014), both months of November 2008 (Max=246cm, Mean=214cm, Min=184cm) and July 2009 (Max=790cm, Mean=753cm, Min=718cm) had water levels similar to the respective months of 2013 (July: Max=726cm, Mean=690cm, Min=654cm; November: Max=296cm, Mean=275cm, Min=246cm). The band composition (5,4,3 in RGB composition) and image analysis were made through the commercial software ArcGis 9.2.

2.6. Variables calculated

The Index of Relative Importance (IRI) modified by Pinkas et al. (1971) was used to determinate the importance of each species caught by the riverine communities. The IRI was calculated as follows:

$$IRI_i = (N_i + W_i) FO_i$$

, where N_i is the numerical percentage of the i th species in all fish landings, W_i is the weight percent of the i th species in all fish landings and FO_i is the frequency of occurrence percentage of the i th species in all fish landings.

We used the IRI to calculate an Indicator of Valuable Fish Presence (IVFP) in each lake according to the equation:

$$IVFP_k = \sum IRI_i RA_{ki}$$

, where IRI_i is the Index of Relative Importance of the i th fish and RA_{ki} is the relative abundance of the i th fish in the k th lake. High values of IVFP in a lake suggests a great proportion of species relevant for fisheries, which have higher IRI values.

The species richness was estimated for each lake through individual-based rarefaction procedure (Gotelli and Colwell, 2011). The trophic position of each species caught in the studied lakes was determined according to the equation:

$$TL_i = 1 + \sum DC_{ij} TL_j$$

, where DC_{ij} is the fractions of each j th prey in the diet of the i th predator and TL_j is the trophic level of the j th prey (Pauly et al., 2001). The trophic level of basal itens ingested (Detritus, Plant, Algae) was considered 1, invertebrates ingested were considered 2 and fish ingested was considered 3 (Hoeinghaus, 2009). Thereafter, we used the TL of each species to calculate the mean trophic level (MTL) of each lake according to the following equation:

$$MTL_k = \sum TL_i RA_{ki}$$

, where TL_i is the trophic level of the i th fish and the RA_{ki} is the relative abundance of the i th fish in the k th lake (Pauly et al., 2001).

2.7. Data analysis

2.7.1. Fishing pressure

The fish landings from the riverine communities were grouped in four main seasons according to the water level: *Seca* (low water), *Enchente* (rising water), *Cheia* (high water) and *Vazante* (falling water). The total biomass of fish caught and the biomass catch per unit effort –CPUE (fish biomass divided by the number of fishermen and the time spent fishing) – were used to assess fishing pressure of each fisherman in each season. The linear mixed effects analysis were carried out to test the influence of CU over fish landings (total biomass and CPUE of biomass) during these four main seasons. Areas (FLONA, RESEX and the unprotected area) and seasons were entered into the model as fixed effects, whereas fisherman was entered as a random effect. The factors significance (P- values) were obtained by likelihood ratio tests comparing models with and without the variables of interest (Winter, 2013). The mixed model analysis was conducted with two datasets: 1) Fish landings from both lakes and the main river; 2) Fish landings only from lakes. This was necessary to understand the effects of fishing on these two environments, since previous studies suggest a high connectivity between fish assemblages of lateral lakes and the main river channel in the Amazon (Fernandes, 1997; Winemiller and Jepsen, 1998). Both total biomass and the CPUE were log transformed to meet normal distribution

assumption. The linear mixed effects analysis was carried out in the R package lme4 (Bates et al., 2014).

2.7.2. *Fish assemblage and environmental variables*

The model averaging (Burnham and Anderson, 2002) was used to obtain robust estimates of relative importance value (I) for both environmental variables (pH, conductivity, depth, euphotic zone, surface size of the lake, shoreline development, percentage of macrophytes, percentage of flooded forest, percentage of pelagic zone, distance from the Lower Amazon River) and management variables (protected or unprotected areas). These independent variables were used as predictors for each one of the dependent variables: fish biomass, richness, abundance, mean size, MTL and IVFP, for each season (high water and low water). The model averaging was carried out according to the following steps: 1) all possible models (linear) were fitted to data; 2) the second order Akaike Information Criterion (AICc) was used to measure the plausibility of each candidate model; 3) The Akaike weight was calculated for each model (w_i) normalized across the set of candidate models to sum to one; 4) The Akaike weights were used to obtain averaged estimates for each parameter; 5) The relative importance of each predictor variable was calculated by summing all Akaike weights over all models that include each predictor. The relative importance ranges from 0 to 1, and the larger the value of the relative importance of a predictor, the more important it is compared to the others (Burnham and Anderson, 2002). To avoid multicollinearity between predictors, the Principal Component Analysis (PCA) was carried out to group the following variables into principal components axis in both seasons: 1) the percentage of pelagic zone, flooded forest and macrophytes; 2) Conductivity, pH, depth and euphotic zone. A Pearson correlation was carried out between predictors and descriptors to assess the direction (negative or positive) and slope of each relation. The biomass was log transformed to meet normal distribution assumption. The model averaging procedure was conducted in the R package glmulti (Calcagno, 2013), whereas the PCA in the package stats (R Core Team, 2014).

The nonmetric multidimensional scaling (NMDS) was used to assess the variation in fish composition among the 12 sampled lakes in each season. This ordination was carried out through two axis using the Bray–Curtis dissimilarity. The environmental and management predictors were correlated onto the NMDS ordination using vector fitting, which quantify the strength of relationships through the correlation coefficient (r^2 ; Oksanen, 2013). Only the predictors that had high influence in the model averaging

procedure were included in this step. The significance (P value) between the ordination and the predictors was assessed after 10000 permutations. Both the vector fitting and the NMDS ordination were carried out in the R package *vegan* (Oksanen et al., 2009).

3. Results

3.1. Fishing pressure

A total of 18,241 kg of fish were caught in the fish landings registered by local fishermen during the study (~ 9.07 kg per landing, SD=12.74). From the 2,013 fish landings registered, 67.2% occurred in the main river, while 32.8% occurred in lakes (Table 2). The jaraqui (*Semaprochilodus* spp.; IRI= 6.68), pescada (*Plagioscion* spp.; IRI= 6.35), aracu (Anostomidae; IRI= 4.82), charuto (Hemiodontidae; IRI=4.68), acaratinga (*Geophagus surinamensis*; IRI=3.85) and tucunaré (*Cichla* spp.; IRI=1.14) were the main fish caught by fishermen (more details in Tables 2 and Hallwass et al., in press).

The exclusion of the interaction term between season and areas in the model resulted in a significant loss of variance explanation from both CPUE ($\chi^2(6)= 1417.7$ P<0.001) and total biomass ($\chi^2(6)= 34.053$ P<0.001) of fish caught by fishermen in both environments (lakes and the main river). Corroborating the first hypothesis, the total biomass caught by fishermen was higher in the unprotected area than in the protected ones in all seasons (Fig. 2b), except during the falling water season when the RESEX had total caught similar to the unprotected area. Inside protected areas, the total fish biomass caught by fishermen from FLONA was smaller than those caught by fishermen from RESEX, except in the high water season when fishermen from FLONA caught more fish (Fig. 2b). As predicted by the second hypothesis, the CPUE was lower in communities located in the unprotected area than in communities located in the protected areas, except during the low water season, when the CPUE was similar between the areas (Fig. 2a). The communities inside the two protected areas, FLONA and RESEX, had similar values of CPUE, except during the falling waters, when RESEX had higher CPUE values (Fig. 2a). When considering only fish landings from lakes, the CPUE did not differ between protected and unprotected areas ($\chi^2(6)= 0.29$ P>0.05; Fig. 2c), while the interaction term between season and areas was significant for the total biomass ($\chi^2(6)=18.6$ P=0.004; Fig. 2d). Overall, lakes from protected areas were less fished (had lower total fish biomass) than lakes from unprotected area, except in the falling water when protected areas and the unprotected area had similar values.

Table 2

The popular name, frequency of occurrence, number of individuals, total weight and the origin (lake or main river) of fishes found in the landings from the low Tapajós River, Amazon. This list includes only those taxa that composed at least 1% of the total weight.

Taxa	Popular name	frequency of occurrence (%)	Number of individuals	Total Weight (Kg)	Origin	
					Lakes (%)	Main River (%)
<i>Geophagus surinamensis</i>	Chaperema, acaratinga	20	9411	868.93	33.13	66.87
Anostomidae	Aracu	20	8319	1922.61	50.81	49.19
Curimatidae	Branquinha, jaraquirana, jaraqui branco	7	1948	209.05	54.48	45.52
<i>Brachyplatystoma rousseauxii</i>	Dourada	3	393	776.15	1.69	98.31
<i>Brachyplatystoma filamentosum</i>	Filhote	6	351	934.3	0	100
<i>Semaprochilodus insignis</i>	Jaraqui	18	12349	3050.83	56.84	43.16
<i>Hypophthalmus spp.</i>	Mapará	9	2048	633.76	9.44	90.56
<i>Brycon falcatus</i>	Matrinchã, jatuarana	1	422	155.4	52.38	47.62
<i>Myleus spp., Mylossoma spp., Metynnis spp.</i>	Pacu	7	1609	232.97	53.79	46.21
<i>Plagioscion squamosissimus</i>	Pescada	25	8838	1926.2	11.71	88.29
Hemiodontidae	Charuto, piraruiira	11	21772	1626.1	30.98	69.02
<i>Pellona spp.</i>	Sarda	10	1721	689	13.94	86.06
<i>Cichla spp.</i>	Tucunaré	15	1156	925.59	41.9	58.1

3.2. Environmental variables and fish assemblages

There was a high variability in the structure, morphology and physical-chemical parameters among the studied lakes (Supplementary data - B). The percentage of pelagic zone, flooded forest and macrophytes (herein called “habitat coverage”) were successfully reduced into a principal component analysis for the high water and low water seasons. The Habitat Coverage PC1 explained 78% of total variation in the high water season and 85% in the low water season (Table 3). On the other hand, the conductivity, pH, depth and euphotic zone (herein named Physical and Chemical Parameters) were reduced into a principal component in the high water season (explaining 69% of total variation; Table 3) and two in the low water season (explaining 48% and 33% respectively; Table 3).

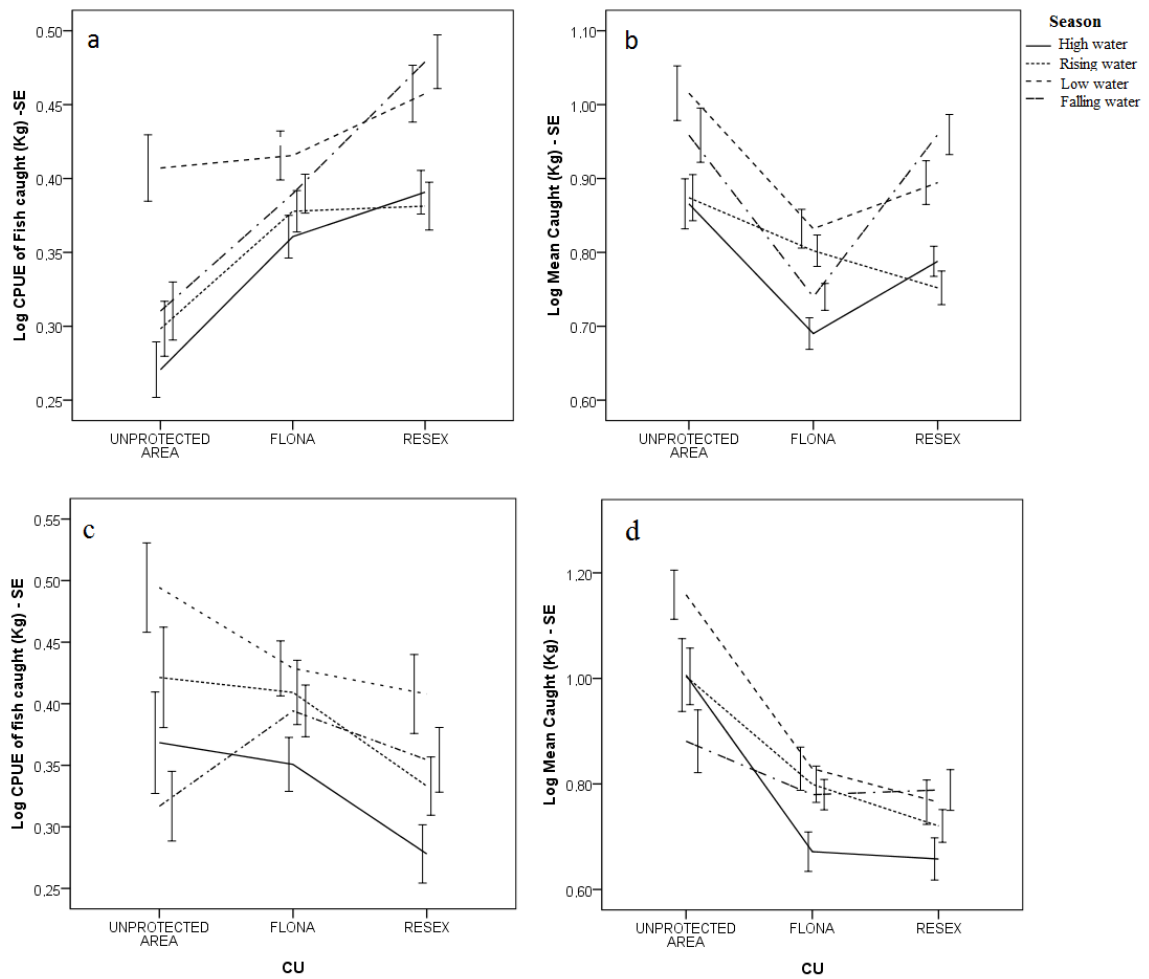


Fig. 2. Fish caught by fishermen in the main river and lakes in each conservation unit (CU) – FLONA, RESEX and unprotected Area - during the four main seasons of the year (High water, rising water, low water and falling water), considering a) CPUE (biomass of fish/hour * number of fishermen) in the main river and lakes, b) total biomass in the main river and lakes, c) CPUE in lakes only, d) total biomass in lakes only.

Table 3

Scores of PCA carried out for habitat coverage (macrophytes, flooded forest, pelagic habitat) and physical and chemical (conductivity, pH, depth and euphotic zone) parameters in the low and high water period. The percentage of explanation of each axis is given in the text.

Habitat coverage			Physical and Chemical Parameters			
Variables	High water	Low water	Variables	Low water	High water	
	PC1	PC1		PC1	PC2	PC1
Macrophytes	-0.03	-0.65	conductivity	-0.39	-0.51	-0.44
flooded forest	0.72	-0.10	pH	-0.15	0.79	-0.55
pelagic habitat	-0.68	0.75	Depth	0.65	-0.27	-0.50
			euphotic zone	-0.62	-0.15	0.50

A total of 879 fish of 67 different species were collected (Table 4): 334 fish (30 species) were caught in the high water season and 545 (56 species) in the low water season. The collected fish range from 1 g (5.7 cm) to more than 5 kg (1.1 m), while the mean trophic level (MTL) ranged from 2.3 to 3.39. According to the model averaging process, the CU (Fig. 3) were one of the most important variables to describe the variation of the following three descriptors of fish assemblage: mean fish size in the high water season (I=1) and MTL (I=0.88) and IVFP (I=0.9) in the low water season (Details in Table 5). However, the fish size, MTL and IVFP were not consistently higher inside CUs as expected by the hypothesis 3 (Fig. 3 d, e, f, respectively). On the other hand, environmental variables showed to be substantial predictors of five descriptors (Abundance, biomass, fish size, MTL, and richness; Table 5). More specifically, the surface size of the lake was an important descriptor for richness in the dry season (I=0.87, Correlation=0.63). The shoreline development was one of the best predictor of abundance (I=0.75, Correlation = -0.59) and mean fish size (I=0.86, Correlation= 0.26) in the wet season. The Physical-Chemical parameters that were reduced into a PCA1 in the wet season turn out to be an important predictor to explain the variation of the MTL (I=0.99, Correlation= -0.80). The first axis of Physical-Chemical parameters of low water season was the best predictor to explain both biomass (I=0.82, Correlation=-0.62) and abundance (I=0.87, Correlation=-0.69), while the second axis was important to explain richness (I=0.53, Correlation=0.57). The principal component (PC1) of habitat coverage was an important descriptor of abundance in the wet season (I=0.65, Correlation=-0.51) and of biomass (I=0.74, Correlation=-0.58) in the dry season. Finally, the distance to Amazon River was not an important predictor to any descriptors of fish assemblage in both seasons. The best models according to AICc for fish assemblage descriptors (Total Biomass, Richness, Abundance, Mean Length, MTL and IVFP) are in Table 6.

Table 4

Fish sampled in floodplain lakes of Tapajós River. Index of Relative Importance (IRI) for fisheries, trophic level (TL) and mean standard length (SL) is shown for each species.

Taxa	IRI	TL	Mean SL (min-max)	Season						
				High Water			Low Water			
				FLONA	RESEX	Unprotected	FLONA	RESEX	Unprotected	
Potamotrygonidae										
<i>Potamotrygon aff. Hystrix</i>	0	3.2	35	0	0	0	1	0	0	0
Engraulidae										

Taxa	IRI	TL	Mean SL (min-max)	Season						
				High Water			Low Water			
				FLONA	RESEX	Unprotected	FLONA	RESEX	Unprotected	
<i>Lycengraulis batesii</i>	0	3	6.62 (5.7 - 6.3)	0	1	0	0	4	0	
Pristigasteridae										
<i>Pellona castelnaeana</i>	0.7	3.8	40.93 (31.5 - 56.5)	2	1	2	1	0	0	
Erythrinidae										
<i>Hoplias malabaricus</i>	0	3.9	25.56 (20.5 - 36.2)	0	0	0	0	4	2	
Ctenoluciidae										
<i>Boulengerella cuvieri</i>	0	4	24.71 (22.5 - 28.7)	3	0	0	3	0	2	
<i>Boulengerella maculate</i>	0	3.9	24.98 (17.4 - 28.5)	0	0	5	8	19	8	
Chilodontidae										
<i>Caenotropus labyrinthicus</i>	0	2	14.32 (13.8 - 15.2)	0	0	0	0	0	4	
Hemiodontidae										
<i>Hemiodus argenteus</i>	4.69	2	15.39 (11.6 - 18.6)	0	3	2	1	0	5	
<i>Hemiodus goeldii</i>	4.69	2	12.85 (8.5 - 17.5)	27	0	0	68	0	28	
<i>Hemiodus cf. gracilis</i>	4.69	2	12.53 (11.2 - 14.3)	0	0	30	0	0	3	
<i>Hemiodus immaculatus</i>	4.69	2.5	13.44 (11.3 - 19.1)	7	2	82	4	0	9	
<i>Hemiodus microlepis</i>	4.69	2.3	16.6	0	0	0	0	0	1	
<i>Hemiodus unimaculatus</i>	4.69	2	13.56 (10.4 - 19.7)	7	16	7	1	0	1	
<i>Anodus orinocensis</i>	4.69	1.8	22.02 (21.7 - 22.6)	0	0	0	0	0	4	
<i>Anodus</i> sp1.	4.69	2.4	11.63 (11.4 - 12)	0	0	0	0	3	0	
<i>Argonectes robertsi</i>	4.69	2.6	19.38 (11.8 - 27.5)	4	4	0	0	1	0	
<i>Micromisichodus sugillatus</i>	4.69	2.2	14.3 (12.9-15.4)	6	0	0	0	0	0	
Curimatidae										
<i>Curimatella alburna</i>	0.27	2	9.25 (8.5 - 10.4)	0	0	0	5	1	0	
<i>Curimata inornata</i>	0.27	2	16.25 (15.3 - 17.2)	0	0	0	1	0	1	
<i>Curimata cf. ocellata</i>	0.27	2.5	13.62 (12.2 - 15)	2	0	0	2	0	0	
<i>Curimata vittata</i>	0.27	2	13.15 (9.7 - 16.5)	0	0	0	0	0	8	
<i>Cyphocharax abramoides</i>	0.27	2	11.72 (9 - 17.6)	0	0	0	3	7	11	
<i>Potamorhina latior</i>	0.27	2	19.1	0	0	0	1	0	0	
Prochilodontidae										
<i>Semaprochilodus insignis</i>	6.68	2	21.26 (19.5 - 23.3)	1	1	0	0	0	1	
Anostomidae										
<i>Leporinus affinis</i>	4.83	2.7	20	0	0	0	0	0	1	
<i>Leporinus fasciatus</i>	4.83	2.6	14.3 (10.9 - 22.6)	0	2	3	0	1	2	
<i>Schizodon fasciatus</i>	4.83	2.1	19.7	0	0	0	3	0	1	
<i>Schizodon vittatus</i>	4.83	2.1	25.5	0	0	0	0	0	1	
<i>Laemolyta proxima</i>	4.83	2	14.58 (12.3 - 18.8)	0	0	0	10	6	0	
Acestrorhynchidae										
<i>Acestrorhynchus falcirostris</i>	0	4	20.54 (8 - 28)	0	0	0	15	15	1	
<i>Acestrorhynchus microlepis</i>	0	4	18.44 (9 - 35.5)	1	0	0	0	14	14	
Serrasalmidae										
<i>Serrasalmus elongatus</i>	0.01	3.8	13.9	0	0	0	0	0	1	
<i>Serrasalmus spilopleura</i>	0.01	3.2	15.9 (11.5 - 19)	0	0	0	1	6	0	
<i>Serrasalmus</i> sp1.	0.01	3.1	10 (8.5 - 11.5)	0	0	0	0	2	0	

Taxa	IRI	TL	Mean SL (min-max)	Season					
				High Water			Low Water		
				FLONA	RESEX	Unprotected	FLONA	RESEX	Unprotected
<i>Serrasalmus</i> sp2.	0.01	3.1	10.4	0	0	0	0	1	0
<i>Colossoma macropomum</i>	0.01	2.2	18.6	1	0	0	0	0	0
<i>Myleus torquatus</i>	0.26	2	15.1	0	0	1	0	0	0
<i>Metynnis lippincottianus</i>	0.26	2	6.75 (6.5-7)	0	0	0	0	2	0
<i>Catoprion mento</i>	0.01	3.2	9	0	0	0	0	1	0
Triporthidae									
<i>Agoniates halecinus</i>	0	3.9	12.96 (12 - 14)	0	0	0	0	5	0
<i>Triporthes auritus</i>	0	2.3	16.35 (12.7 - 20)	0	0	0	0	0	2
<i>Triporthes rotundatus</i>	0	3.2	15.3	0	0	0	0	1	0
Iguanodectidae									
<i>Bryconops alburnoides</i>	0	3	13.88 (12.9 - 15.5)	5	1	1	2	0	1
<i>Bryconops caudomaculatus</i>	0	3	6 (5.7 - 6.3)	0	0	0	1	0	1
<i>Bryconops giacopinii</i>	0	3	10.6	0	1	0	0	0	0
<i>Bryconops melanurus</i>	0	3	9.9	0	0	0	0	1	0
Bryconidae									
<i>Brycon cf. pesu</i>	0	2.7	9.92 (8.5 - 11.1)	0	9	10	1	0	3
Pimelodidae									
<i>Pseudoplatystoma tigrinum</i>	0.01	3.8	28 (26-30)	0	0	0	0	2	0
<i>Leiarius marmoratus</i>	0	4	18.4	0	0	0	0	1	0
<i>Hypophthalmus marginatus</i>	0.61	3	43.63 (41.5 - 45)	0	1	3	0	0	0
Callichthyidae									
<i>Hoplosternum littorale</i>	0	3	13.83 (13 - 14.5)	0	0	0	0	3	0
Loricariidae									
<i>Ancistrus</i> sp.	0	2	10.1	0	1	0	0	0	0
<i>Limatulichthys griseus</i>	0	2.2	22.56 (20.5 - 24.2)	0	0	2	0	0	1
<i>Loricariichthys acutus</i>	0	2.4	21.06 (17.5 - 24)	0	0	0	0	26	2
<i>Loricariidae</i> sp.	0	2.2	27.2	0	0	0	1	0	0
Doradidae									
Doradidae sp.	0	2.5	8.3	0	0	0	0	1	0
Gymnotidae									
<i>Electrophorus electricus</i>	0	3.4	110	1	0	0	0	0	0
Cichlidae									
<i>Acarichthys heckelii</i>	0	2.8	9.62 (6.1 - 14.1)	8	3	1	21	13	10
<i>Cichla monoculus</i>	1.14	3.8	27.25 (22.5 - 32)	0	0	0	0	2	0
<i>Cichla pinima</i>	1.14	3.9	15.33 (7.3 - 57)	8	13	19	2	9	9
<i>Crenicichla marmorata</i>	0	3.2	17	0	0	1	0	0	0
<i>Geophagus surinamensis</i>	3.86	2.6	12.51 (6.8 - 20)	3	3	4	1	1	14
<i>Mesonauta festivus</i>	0.01	2.4	9.2 (6 -11)	0	0	0	0	7	0
<i>Satanoperca acuticeps</i>	0	2.9	10.02 (6.8 - 13.6)	0	0	0	3	34	1
<i>Satanoperca jurupari</i>	0	3	18.68 (11.8 - 24.5)	8	0	0	22	8	0
<i>Uaru amphiacanthoides</i>	0.01	2.1	17.75 (15.5 - 22)	5	0	0	8	0	0
Sciaenidae									
<i>Plagioscion squamosissimus</i>	6.35	3.3	21.3	0	0	0	0	0	1

Table 5

Model-averaged importance of predictors (I) for the dependent variables Biomass, Richness, Abundance, Mean size, MTL (Mean Trophic Level) and IVFP (Indicator of Valuable Fish Presence) for both wet and dry season in the Tapajos River. Bold values indicate the more important terms.

High water season						
	Biomass	Richness	Abundance	Mean Size	MTL	IVFP
Surface size of the Lake	0.09	0.13	0.07	0.04	0.07	0.13
Amazon distance	0.13	0.17	0.10	0.04	0.07	0.11
Shoreline development	0.20	0.33	0.75	0.86	0.12	0.11
Conservation units	0.28	0.11	0.09	1.00	0.13	0.11
Physical-Chemical parameters (PCA1)	0.31	0.16	0.09	0.19	0.99	0.12
Habitat coverage (PCA1)	0.42	0.14	0.65	0.23	0.23	0.40

Low water season						
	Biomass	Richness	Abundance	Mean Size	MTL	IVFP
Surface size of the Lake	0.06	0.87	0.08	0.11	0.09	0.14
Amazon distance	0.07	0.08	0.08	0.11	0.35	0.11
Shoreline development	0.09	0.10	0.07	0.21	0.09	0.07
Conservation units	0.13	0.16	0.20	0.10	0.88	0.90
Physical-Chemical parameters (PCA1)	0.82	0.11	0.87	0.11	0.13	0.17
Physical-Chemical parameters (PCA2)	0.07	0.53	0.08	0.12	0.07	0.07
Habitat coverage (PCA1)	0.74	0.39	0.09	0.10	0.11	0.10

Table 6. Best models for total biomass, richness, abundance, mean size, MTL (Mean Trophic Level) and IVFP (Indicator of Valuable Fish Presence) according to AICc weight. The constant 1 included in all models is the intercept. The absence of independent variables indicates that the best model according to AICc weight was that one with no predictors.

Response variables	Best models – High water season	AICc Weight
Biomass	1	0.14
Richness	1	0.25
Abundance	1+ Shoreline development + Habitat coverage (PCA1)	0.43
Mean Size	1+ Conservation units + Shoreline development	0.49
MTL	1+ Physical-Chemical parameters (PCA1)	0.47
IVFP	1	0.27

Response variables	Best models – Low water season	AICc Weight
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Biomass	1+ Physical-Chemical parameters (PCA1) + Habitat coverage (PCA1)	0.44
Richness	1+ Surface size of the Lake + Physical-Chemical parameters (PCA2)	0.23
Abundance	1+ Physical-Chemical parameters (PCA1)	0.44
Mean Size	1	0.35
MTL	1+ Conservation units	0.33
IVFP	1+ Conservation units	0.44

The NMDS ordinations of lakes according to fish assemblage (Fig. 4) had stress values lower than 0.15 (Wet = 0.11, Dry = 0.14), which indicated a reliable pattern. There were marginally significant relationships between the first principal axis of the physical-chemical parameters ($p=0.069$, $r^2=0.45$) and the habitat coverage ($p=0.059$, $r^2=0.46$) with fish assemblage in the wet season. In relation to the dry season, the first axis of physical-chemical parameters had significant influence ($p=0.01$, $r^2=0.65$) over fish assemblage, while the protected areas had just marginally significant relationship ($p=0.057$, $r^2=0.35$).

4. Discussion

4.1. Fishing pressure and conservation units

Like most CUs that include freshwater ecosystems, both FLONA and RESEX were not specifically designed to protect freshwater ecosystems and their associated organisms. Instead, FLONA and RESEX were created to protect the Amazon forest from logging (IBAMA, 2004; ICMBIO, 2008). Nevertheless, lakes and the river in the unprotected area were more intensely fished (had a higher total biomass of fish caught) than protected areas. Besides, fishermen from the unprotected area also spent more time and labor fishing (had a lower CPUE) than fishermen from the two protected areas. These results agreed with our hypotheses and indicate that the conditions provided by the protected areas in the Tapajós River, such as lower human population density, general management rules and higher environmental integrity (eg. less pollution and deforestation), may act synergistically to reduce the levels of fishing pressure and increase the density of target fish.

Even with lower levels of fishing and higher abundance of fish, FLONA and RESEX may not be capable to conserve and maintain a great portion of fish stock in the Tapajós River alone. Overall, the role of CU for fish protection depend on fish movement and the size of the protected area: sedentary animals tend to be more protected by CUs than those that constantly cross the boundaries of protected areas (Palumbi, 2004; Baird and Flaherty, 2005). In tropical rivers, which typically have high variation in hydrological

regime, the key biological factor behind the maintenance of high diversity of fish species is movement (Lowe-McConnell, 1999). Most fish species of Amazon undertake lateral (Fernandes, 1997) or longitudinal (Barthem and Goulding, 1997; Carolsfeld et al., 2004) migrations at least once in their life cycle (Winemiller and Jepsen, 1998; Lowe-McConnell, 1999). In oligotrophic waters, such as the Tapajós River, the role of migratory species to sustain fisheries is vital. Species from several families of characiformes and siluriformes migrate from rich nutrient waters to poor nutrient waters in specific seasons to feed and spawn (Carolsfeld et al., 2004), increasing the secondary productivity of oligotrophic rivers and consequently the income of fishermen (Barthem and Goulding, 1997, 2007). Fisheries in the Tapajós River include species that perform long migrations, such as *Brachyplatystoma rousseauxii*, *B. filamentosum* and *Semaprochilodus insignis*. Therefore, to ensure the maintenance of fisheries and the conservation of biodiversity in the Tapajós River, as well as in other tropical rivers, it is necessary to create a network of CUs in strategic points of spawning and feeding areas in a broad scale, and ensure connectivity between rivers with poor and rich waters (Barthem and Goulding, 1997; Pelicice et al., 2014).

In a fishing perspective, it would be desirable that protected areas become a source of fish population to support human harvesting in the surroundings. For example, in the Mekong basin at least eight species of fish spill over from Freshwater Conservation Zones (FCZs) to nearby regions, contributing to local fisheries (Ounboundisane et al., 2013). Similarly, in a co-management perspective, it has been suggested that non-fished lakes may be a source of fish for fished lakes in a sustainable CU in the Brazilian Amazon (Silvano et al., 2009). However, it is not necessarily true that just because an area is not fished (or less fished) it would become a source of fish for other areas. In many cases, CUs are established in unproductive areas with low commercial interest (Scott et al., 2001; Hansen, 2011). Therefore, these habitats may have harsher biophysical conditions for organisms, being a sink instead of a source of biomass (Hansen, 2011). In Tapajós River, the observed high levels of CPUE in CUs indicated higher fish density in protected areas, however it is difficult to determine if there is a spillover effect. Similar to most regions in the world (Geisler, 1993; Guidetti, 2002), the Tapajós River lacks studies from before the establishment of CUs, which could elucidate the effect of protected areas as sources of biomass for fisheries in unprotected regions. Currently, there is a gap of information in relation to the spillover effect of CUs in the Tapajós River as well as in other freshwater

ecosystems worldwide. Future studies aiming to quantify the spillover effect in freshwater ecosystems will find an unknown and prosperous research field in the next years.

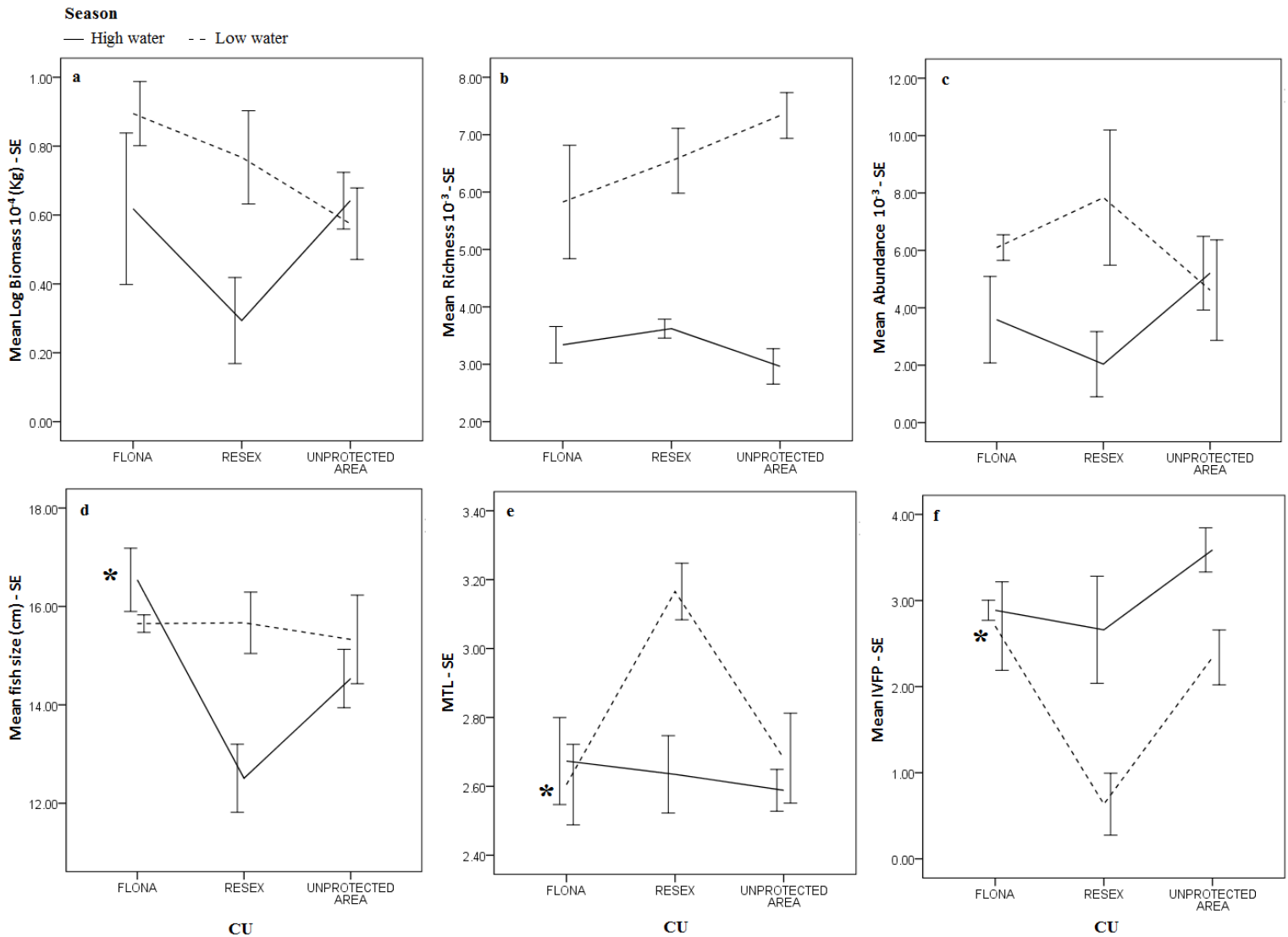


Fig. 3. The a) mean biomass, b) mean richness, c) mean abundance, d) mean fish size, e) MTL (Mean Trophic Level) and f) IVFP (Indicator of Valuable Fish Presence) between the conservation units (UC) in the high water and low water season. Asterisks (*) symbolize high importance according to the model averaging approach.

The two protected areas (FLONA and RESEX) differed in fishing pressure and CPUE in at least two seasons (low water and falling water). Fishermen from RESEX had higher values of both CPUE and total biomass. It is likely that these differences between FLONA and RESEX are consequences of differences in management rules and environmental characteristics. Although management rules related to fishing equipments are similar in both CUs, the fish commercialization is just allowed in RESEX (ICMBIO, 2008), which led fishermen to intensify the capture of fish and consequently their incomes

(Hallwass et al., in press). Besides, the main depth channel of Tapajós River is located near to RESEX's shorelines (Hallwass et al., in press). According to local fishermen, this depth channel is an important fishing spot to catch important target species with large size, such as pescada (*Plagioscion* spp.) and filhote (*B. filamentosum*) (Hallwass et al., in press).

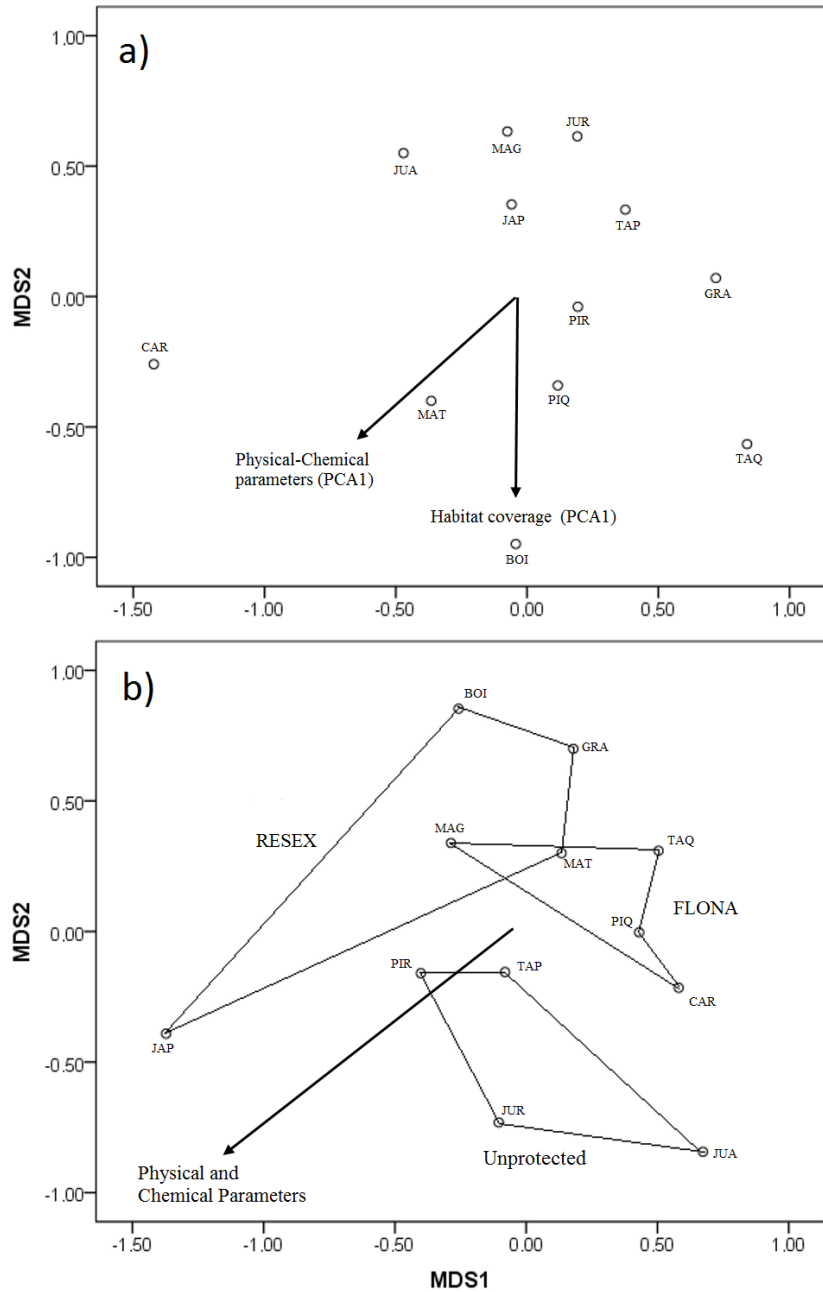


Fig. 4. Results from the nonmetric multidimensional scaling analysis (NMDS) of the lakes in the high water (a) and low water (b) season according to their fish assemblage. Arrows and polygons represent variables which were correlated significantly or marginally significantly to the fish assemblage. Each code (eg. TAQ) represents a lake, which can be consulted in table 1 for more specific details.

4.2. Effect of CU over fish assemblage in floodplain lakes

Although fishermen from the two CUs had a higher CPUE than fishermen from fishing communities in the unprotected area, no effect of CUs was found on fish landings originated from floodplain lakes. These results were similar to results from experimental fish samples carried out in the floodplain lakes: Fish community descriptors, such as the biomass, abundance and richness, were similar between the two CUs and the unprotected area. On the other hand, the biological attributes of fish assemblages were more related to environmental variables (shoreline development, physical-chemical parameters, habitat coverage and surface size). Although some variation in mean fish size, mean trophic level and the presence of valuable fish were found among CUs, smaller values of these parameters were not identified in the unprotected area, as expected. For example, the mean trophic length (MTL) was higher in RESEX's region, but the FLONA's region (protected area) had a MTL similar to that observed in the unprotected area in the dry season. Interestingly, the IVFP was the inverse in this period, with RESEX's region with smaller values than FLONA and the unprotected area. This unexpected negative relation between MTL and IVFP resulted from a high preference for fish with low trophic level, such as charuto (Hemiodontidae family), jaraqui (*Semaprochilodus* spp.) and aracu (Anostomidae family) in the Tapajós small-scale *fisheiros*.

The observed low influence of CUs on fish assemblages in lakes may be due to the low levels of fishing in this habitat, as most of fish registered in fish landings were caught in the main river channel. Therefore, the fishing impact (eg. lower CPUE) could be more evident in the main river channel than in floodplain lakes. Such preference for the main river channel instead of floodplain lakes differs from what was observed in productive rivers with white water in the Brazilian Amazon, such as the Solimões River, where fisheries are usually concentrated in lakes, at least during the low water season (MacCord et al., 2007). The floodplain of Tapajós River, including the abundance and size of floodplain lakes, is smaller than that of other rivers of the same order in the Amazon Basin (Goulding et al., 2003). Besides, the mean fish density ($0.54 \text{ g} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$, standardized CPUE) found in floodplain lakes of Tapajós River was low compared to other Amazonian rivers sampled using comparable methodology, such as Japurá and Solimões (22.4 g and 13.5 g, Henderson and Crampton 1997; Silvano et al., 2009, respectively), Manacapuru (14.5 g, Saint-Paul et al. 2000), Mucajá (3.7 g, Ferreira et al. 1988), Lower Tocantins (5 g and 2.84 g, De Merona, 1986/87; Silvano et al., 2014, respectively), Trombetas (10.2 g, Ferreira, 1993) and Negro (2.69 g, Silvano et al. 2005). Therefore, the floodplain lakes of

Tapajós River may be less attractive for fishermen compared to lakes in other rivers, due to the low density of fish. Nevertheless, differences in fish species composition between lakes and the main river channel may also have contributed to the discrepancy between results from fisheries and the fish assemblage in lakes. Abundant target fish, such as *Pellona* spp., *Plagioscion* spp., *Hypophthalmus* spp., *B. filamentosus* and *B. rousseauxii* were almost exclusively caught by fishermen in the main river, indicating their low density in floodplain lakes.

The absence of CU effects on fish assemblages in floodplain lakes may also be result of management in a small scale. The co-management is a coalition of local riverines, who create rules to avoid local resource overexploitation and protect the resource from outsiders (MacCord et al., 2007, Lopes et al., 2011). Although this co-management activity are rarely recognized as a legal activity by the government, surveys have been suggested that these local coalition can have good results to maintain or increase the resources productivity and sustainability in tropical developing countries (Cinner et al., 2005; Sultana and Thompson, 2007; Silvano et al, 2014). In the Tapajós River, evidences from interviews with fishermen suggest that some riverine communities have local rules regarding fish harvesting (Hallwass et al., in press). From the 12 studied communities, two communities from unprotected area (Maracanã and Alter do Chão), one from FLONA (Pini) and two from RESEX (Jauarituba and Vila do Amorim) have some initiative of co-management in adjacent lakes (Hallwass et al., in press). Although the co-management effect have never been checked in the Tapajós River, Silvano et al. (2014) demonstrated that for Tocantins River, other clear water river from Amazon, the co-management influence positively fishing yields of fishing communities and fish abundance in floodplain lakes.

4.3. Effect of environmental variables on fish assemblages

Floodplain lakes from Tapajós River showed high environmental heterogeneity in space and time. This variability led to different association of fish assemblages as have already been suggested by several studies in the Amazon basin (Junk et al., 1983; Rodriguez and Lewis, 1997; Tejerina- Garro et al., 1998; Petry et al., 2003). The physical-chemical parameters (depth, conductivity, euphotic zone and pH) were the most important environmental variables, influencing the trophic level, biomass, richness, abundance and composition of fish in the Tapajós River. Depth has been considered the primary controller of the variability observed in the other physical-chemical parameters measured (Rodriguez and Lewis, 1997). In this sense, the results present here confirm the importance of depth to

determine fish assemblage, especially regarding to trophic level (Miranda, 2011) and the number of fish captured (Petry et al., 2003). On the other hand, the surface size of the lake was a good descriptor for richness, indicating a classic species-area relationship (Arrhenius, 1921). There are several hypotheses that explain the species-area relationship, which are not necessarily mutually exclusive but vary in complexity (Neigel, 2003). For example, the random placement hypothesis (MacArthur and Wilson, 1963), the most parsimonious one, suggest a simple effect of sampling, while the habitat heterogeneity hypothesis (Williams, 1943) suggest that larger areas enclose more diverse types of microhabitats and therefore include more species. Anyhow, because to conserve a high number of species is a common goal of management programs (Groom et al. 2005), floodplain areas that include bigger lakes should be prioritized to conserve fish biodiversity.

The habitat coverage influenced the biomass and abundance of fish in floodplain lakes of Tapajós River. More specifically, the percentage of macrophytes was positively related to fish biomass, while flooded forest was negatively correlated with fish abundance. This result corroborate previous studies, which indicate that the environmental heterogeneity provided by the presence of macrophyte banks may promote the diversity and abundance of fish, due to protection and feeding (Petry et al., 2003; Agostinho et al., 2007). In this sense, the maintenance of macrophyte banks in lakes may be important to increase fisheries income directly, increasing the biomass of target fish, or indirectly, being a nursery habitat for juvenile fish or providing a feeding habitat for larger fish. On the other hand, flooded forests are an important source of food in Amazon tributaries that contain oligotrophic waters (Goulding and Ferreira, 1988), such as the Tapajós River. Since the samples were carried out exclusively in the pelagic habitat, the wide extension of flooded forest in the wet season could act as an attractor for fish, decreasing the density of fish in the pelagic zone. Furthermore, lakes with developed shorelines had more contact area with the surrounding forest, and, perhaps, the observed negative correlation between shoreline development and fish abundance may also be influenced by the percentage of flooded forest.

The landscape of floodplains in the Amazon change drastically from season to season, due to changes in the water level of the main river (Junk et al., 1989). Fish respond to this periodic flood pulse through morphological, anatomical, physiological and ethological adaptations (Junk et al., 1989). Consequently, it is likely that the structure of fish assemblages change between seasons (Junk et al., 1997). The results showed in this study indicate that fish assemblages also respond differently to environmental conditions

between the seasons. The biological parameters calculated for fish assemblage (eg. biomass, richness, abundance) were correlated with different environmental variables in the low water and high water season. For instance, the abundance was correlated with shoreline development and habitat coverage in the high water season, while in the low water season it was correlated only with physical-chemical parameters (depth, euphotic transparency). Several factors may operate to induce different responses of fish assemblages to distinct environmental parameters between seasons. The change in fish density between the low and high water season in the Amazon floodplain (Fernandes, 1997; Begossi et al., 1999; Silvano et al., 2000; Cerdeira et al., 2000; MacCord et al., 2007; Cardoso and Freitas, 2008) may affect the response of fish to environmental variables (Arrington et al., 2005). More specifically, as fish assemblage get closed to saturation, through the increase of fish density, the fish assemblage become increasingly non-random due to an increasing importance of species-specific responses to habitat characteristics (Arrington et al., 2005). Besides, the change in fish composition (Fernandes 1997) and in the range of environmental parameters (Junk et al., 1989) between the high water and low water seasons may also determine how fish assemblage vary in the floodplain.

In this study, the fish composition was associated mainly with changes in chemical-physical structure and habitat coverage. Several studies attested that floodplains in Amazon are mosaics where species composition is determined by environmental characteristics peculiar to individual sites (Tejerina-Garro et al., 1998, Petry et al., 2003, Correa et al., 2008, Freitas et al., 2014). In this sense, Amazonian lakes are not equivalents regarding fish species composition, and therefore a successful plan to conserve the fish biodiversity should be large enough to include multiple sites (Freitas et al., 2014). Both FLONA and RESEX are large CUs (> than 589,000 ha) and include lakes with different shapes, habitats and physico-chemical characteristics. Furthermore, the more recent EPAs (APAs in Portuguese) may play an important role in the conservation of floodplain heterogeneity, protecting an even large area of floodplain in the region. On the other hand, in unprotected areas, the management in a small scale could be the best option to control the strong effect of environmental variables and to reduce the fishing pressure, ensuring the stock sustainability in floodplain lakes (Prince, 2003; Castello et al., 2013a). However, to ensure that small scale management occur appropriately, it is fundamental the participation and commitment of local communities and the presence of trained local managers to avoid inadequate decisions (Prince, 2003).

5. Conclusions

The fish landings of riverine communities indicated that fisheries are more intense in the unprotected area than in CUs of sustainable use in the Tapajós River. Besides, fishermen from CUs take less time and labor to caught the same quantity of fish than those from the unprotected area. These results are the first evidence that the conditions provided by CUs act synergistically to reduce the levels of fishing and increase the density of target fish in the Amazon Basin, reinforcing the importance of these protected areas to sustain the socio-ecological systems of small-scale fisheries in the Brazilian Amazon. However, a great proportion of fish used by fishermen are migratory species (eg. *B. rousseauxii*, *B. filamentosum* and *S. insignis*), which may need broader CUs or a network of protected areas. On the other hand, the biological parameters of fish assemblages in the floodplain lakes were more correlated with environmental factors than with the CUs. These results were similar to those found in fish landings from lakes. The CPUE of fishermen in floodplain lakes did not differ between protected and unprotected areas. Differences in fishing pressure between the floodplain lakes and the main river channel and also the effect of small-scale management (co-management) that occur in some lakes may partially explain such absence of effect of CU on fish assemblages in floodplain lakes. Anyhow, the environmental variation between lakes create different association of fish species in floodplains and therefore these variables must be considered in management and conservation program in tropical rivers.

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Supplementary data

A – Number of analysed individuals for trophic position estimation in each species. Information from literature were included when there were less than 10 individuals analysed in our study.

Family	Taxa	N of guts analysed	N of guts included from literature	Reference utilized
Potamotrygonidae	<i>Potamotrygon aff. hystrix</i>	0	102	Vasconcellos and Oliveira, 2011
Engraulidae	<i>Lycengraulis batesii</i>	2	0	-
Pristigasteridae	<i>Pellona castelnaeana</i>	3	8	González and Vispo, 2003
Erythrinidae	<i>Hoplias malabaricus</i>	3	49	Mérona and Rankin-de-Mérona, 2004
Ctenoluciidae	<i>Boulengerella cuvieri</i>	7	8	Sá-Oliveira et al., 2014
	<i>Boulengerella maculata</i>	24	0	-
Chilodontidae	<i>Caenotropus labyrinthicus</i>	3	6	Godoi, 2008
Hemiodontidae	<i>Hemiodus argenteus</i>	7	183	Silva et al., 2008 ^a
	<i>Hemiodus goeldii</i>	63	0	-
	<i>Hemiodus cf. gracilis</i>	18	0	-
	<i>Hemiodus immaculatus</i>	38	0	-
	<i>Hemiodus microlepis</i>	1	13	Mérona and Rankin-de-Mérona, 2004
	<i>Hemiodus unimaculatus</i>	21	0	-
	<i>Anodus orinocensis</i>	4	11	González and Vispo, 2003
	<i>Anodus</i> sp1.	2	11	González and Vispo, 2003
	<i>Argonectes robertsi</i>	6	0	-
	<i>Micromischodus sugillatus</i>	4	1	Freitas, 2007
Curimatidae	<i>Curimatella alburna</i>	4	4	Mérona et al., 2001
	<i>Curimata inornata</i>	0	8	Sá-Oliveira et al., 2014
	<i>Curimata cf. ocellata</i>	1	1	Blanco-Parra and Bejarano-Rodríguez, 2006
	<i>Curimata vittata</i>	7	12	Hawlitcshek et al., 2013
	<i>Cyphocharax abramoides</i>	17	0	-
	<i>Potamorhina latior</i>	0	1	Mérona and Rankin-de-Mérona, 2004
Prochilodontidae	<i>Semaprochilodus insignis</i>	2	23	Hawlitcshek et al., 2013
Anostomidae	<i>Leporinus affinis</i>	1	70	Mérona et al., 2001
	<i>Leporinus fasciatus</i>	7	0	-
	<i>Schizodon fasciatus</i>	0	100	Mérona and Rankin-de-Mérona, 2004
	<i>Schizodon vittatus</i>	0	39	Mérona et al., 2001
	<i>Laemolyta proxima</i>	6	4	Silva, 2006
Acestrorhynchidae	<i>Acestrorhynchus falcirostris</i>	16	0	-
	<i>Acestrorhynchus microlepis</i>	13	0	-
Serrasalminae	<i>Serrasalmus elongatus</i>	0	47	Mérona and Rankin-de-Mérona, 2004
	<i>Serrasalmus spilopleura</i>	5	94	Mérona and Rankin-de-Mérona, 2004
	<i>Serrasalmus</i> sp1.	0	94	Mérona and Rankin-de-Mérona, 2004
	<i>Serrasalmus</i> sp2.	0	94	Mérona and Rankin-de-Mérona, 2004

Family	Taxa	N of guts analysed	N of guts included from literature	Reference utilized
	<i>Colossoma macropomum</i>	1	151	Mérona and Rankin-de-Mérona, 2004
	<i>Myleus torquatus</i>	0	1	Mérona et al., 2001
	<i>Metynnis lippincottianus</i>	1	8	Sá-Oliveira et al., 2014
	<i>Catoprion mento</i>	0	24	Silva, 2006
Triportheidae	<i>Agoniatos halecinus</i>	3	46	Silva, 2006
	<i>Triportheus auritus</i>	1	6	Sá-Oliveira et al, 2014
	<i>Triportheus rotundatus</i>	0	169	Mérona et al., 2001
Iguanodectidae	<i>Bryconops alburnoides</i>	6	322	Silva et al., 2008 ^b
	<i>Bryconops caudomaculatus</i>	1	23	Silva. 2006
	<i>Bryconops giacopinii</i>	0	34	Melo et al., 2004
	<i>Bryconops melanurus</i>	0	22	Melo et al., 2004
Bryconidae	<i>Brycon cf. pesu</i>	13	0	-
Pimelodidae	<i>Pseudoplatystoma tigrinum</i>	1	1	Mérona et al., 2001
	<i>Leiarius marmoratus</i>	0	5	Layman et al., 2005
	<i>Hypophthalmus marginatus</i>	3	2	Mérona and Rankin-de-Mérona, 2004
Callichthyidae	<i>Hoplosternum littorale</i>	3	7	Mérona and Rankin-de-Mérona, 2004
Loricariidae	<i>Ancistrus sp.</i>	0	0	TP adapted from FishBase (closed relatives): Froese and Pauly (editors), 2014
	<i>Limatulichthys griseus</i>	0	0	TP adapted from FishBase (closed relatives): Froese and Pauly (editors), 2014
	<i>Loricariichthys acutus</i>	22	0	-
	<i>Loricariidae sp.</i>	0	0	TP adapted from FishBase (closed relatives): Froese and Pauly (editors), 2014
Doradidae	Doradidae sp.	0	0	TP adapted from FishBase (closed relatives): Froese and Pauly (editors), 2014
Gymnotidae	<i>Electrophorus electricus</i>	0	5	Mérona and Rankin-de-Mérona, 2004
Cichlidae	<i>Acarichthys heckelii</i>	40	0	-
	<i>Cichla monoculus</i>	1	34	Mérona and Rankin-de-Mérona, 2004
	<i>Cichla pinima</i>	39	0	-
	<i>Crenicichla marmorata</i>	0	0	TP adapted from FishBase (closed relatives): Froese and Pauly (editors), 2014
	<i>Geophagus surinamensis</i>	21	0	-
	<i>Mesonauta festivus</i>	6	4	Mérona et al., 2001
	<i>Satanoperca acuticeps</i>	28	0	-
	<i>Satanoperca jurupari</i>	28	0	-
	<i>Uaru amphiacanthoides</i>	11	0	-
Sciaenidae	<i>Plagioscion squamosissimus</i>	0	90	Mérona and Rankin-de-Mérona, 2004

B. Physical-Chemical parameters, morphology and structure measured in each one of the studied lakes. Values on the left represent the high water season, whereas values on the right represent the low water season season (High water- Low water). Area= Protected (FLONA and RESEX) and unprotected (UNPR.) areas, Cond = Conductivity ($\mu\text{S}/\text{cm}$),

Eup. Zone= Euphotic zone(%), Depth (m), Surf. size = Surface size of the Lake (km²), Shor. Dev. = Shoreline development, Macr = Macrophyte coverage (%), Forest= Flooded forest (%), Pelagic = Pelagic habitat (%), Amazon = Distance to Amazon River (km). The pH, conductivity, euphotic zone and depth were shown as mean for all the 12 measures made in each lake.

Lakes	Area	pH	Cond	Eup. zone	Depth	Surf. Size	Shor. Dev.	Macr.	Forest	Pelagic	Amazon
MAG	FLONA	6.5 - 5.1	14.3 - 9.7	50.9 - 64.1	5.4 - 1.2	0.73 - 0.56	4.55 - 6.24	10 - 15	40 - 0	50 - 85	67.37
CAR	FLONA	4.7 - 4.2	8.7 - 7.2	98.5 - 100	1.7 - 1.3	0.27 - 0.10	3.93 - 4.78	30 - 50	30 - 0	40 - 50	72.6
PIQ	FLONA	6.4 - 4.1	15.3 - 11.3	54.1 - 100	4.2 - 1.3	0.15 - 0.07	10.85 - 13.58	10 - 10	40 - 10	50 - 80	87.99
TAQ	FLONA	5.9 - 5.1	15.5 - 12.1	51.1 - 69.8	3.3 - 1.1	0.15 - 0.09	9.03 - 6.52	10 - 30	50 - 20	40 - 50	108.61
BOI	RESEX	5.7 - 4.1	12.2 - 14.2	69.5 - 100	3.9 - 1.3	0.40 - 0.11	12.02 - 11.33	0 - 10	50 - 0	50 - 90	108.92
JAP	RESEX	6.3 - 4.3	13.1 - 7.7	27.3 - 31.0	5.7 - 4.9	0.22 - 0.13	8.78 - 6.60	10 - 10	10 - 0	80 - 90	97.92
GRA	RESEX	5.7 - 6.4	14.0 - 10.8	62.5 - 86.5	3.0 - 0.6	0.17 - 0.09	5.66 - 3.70	20 - 0	30 - 0	50 - 100	80.58
MAT	RESEX	6.6 - 6.1	14.2 - 9.0	56.8 - 77.9	3.3 - 0.7	0.04 - 0.02	6.05 - 4.34	0 - 0	70 - 10	30 - 90	72.76
JUR	UNPR.	6.0 - 5.4	12.2 - 5.7	43.8 - 88.8	4.3 - 1.2	0.26 - 0.13	5.37 - 4.10	0 - 0	30 - 0	70 - 100	39.79
PIR	UNPR.	5.6 - 6.2	13.3 - 8.6	48.0 - 80.8	3.1 - 1.2	0.25 - 0.17	4.86 - 5.25	0 - 0	30 - 10	70 - 90	34.53
TAP	UNPR.	6.0 - 5.5	13.1 - 2.6	45.9 - 61.3	4.6 - 1.6	0.65 - 0.31	5.55 - 5.32	0 - 0	20 - 10	80 - 90	21.47
JUA	UNPR.	5.5 - 4.5	10.5 - 9.8	36.2 - 74.2	4.4 - 0.7	1.09 - 0.55	11.79 - 5.18	20 - 10	10 - 10	70 - 70	6.88

CONSIDERAÇÕES FINAIS

Apesar dos ambientes de água doce estarem entre os ecossistemas mais ameaçados no planeta pelas atividades humanas (Saunders et al., 2002; Abell et al., 2008), existem poucas informações e áreas protegidas voltadas a conservar este tipo de ambiente. Entre as UC existentes que incluem ecossistemas aquáticos, a grande maioria foi criada e delimitada em primeiro lugar para a proteção de ecossistemas terrestres (Rodríguez-Olarte et al., 2011). Conseqüentemente, a maior parte dos ecossistemas de água doce são protegidos de forma fragmentada, sem nenhuma confiabilidade quanto a sua efetividade frente a distúrbios antrópicos (Nel et al., 2007; Gaston et al., 2008; Abraão e Kelkar, 2012). Na Amazônia, a pesca vem sendo considerada como uma das principais atividades humanas influenciando a assembleia de peixes (Santos and Santos, 2005; Castello et al., 2013b). De acordo com as nossas informações, este é o primeiro trabalho que buscou investigar a intensidade e efeito da pesca em áreas protegidas e não protegidas na Amazônia.

Os resultados levantados pelo nosso estudo indicaram que, como esperado pela hipótese 1, áreas protegidas sofrem menor pressão de pesca do que área não protegidas. Além disso, os pescadores de comunidades ribeirinhas dentro das UC em média gastaram menos tempo e menos trabalho (CPUE maior) para capturar a mesma quantidade de peixe do que pescadores localizados fora das UCs, corroborando a nossa hipótese 2. Portanto, as condições fornecidas pelas UCs no Rio Tapajós (menor densidade humana, regras de manejo mais restritas) parecem atuar sinergicamente para reduzir os níveis de pesca, aumentando assim a densidade de peixes de interesse pesqueiro. Estes resultados reforçam o papel das UCs na conservação dos estoques pesqueiros, em um período de descrédito e, conseqüentemente, de desoficialização e diminuição das UCs a nível global (Mascia and Pailler, 2011; Ferreira et al., 2014; Mascia et al., 2014).

O papel de UC para a proteção da ictiofauna depende em última estância da capacidade de movimentação da espécie frente ao tamanho da área protegida (Palumbi, 2004). Espécies que apresentam grande deslocamento e que atravessam as bordas de UC com frequência tendem a ser menos protegidas pela UC do que aquelas que apresentam menor deslocamento e que conseguem complementar todo o seu ciclo de vida dentro da área protegida. Nesse sentido, tanto a FLONA quanto a RESEX sozinhas podem não ser capazes de assegurar a exploração pesqueira a longo prazo, visto que boa parte dos desembarques das comunidades ribeirinhas do baixo Tapajós inclui espécies que realizam

migrações de longa distância (ex: *B. rousseauxii*, *B. filamentosum* e *S. insignis*). Portanto, é sugerido que seja criando redes de UC em pontos estratégicos de reprodução e alimentação em uma escala ampla, assegurando a conexão entre essas diferentes áreas.

É evidenciado a necessidade de novos estudos para compreender o papel das UC como área fonte de pescado para áreas não protegidas. Este processo, conhecido como “spillover effect”, é bem conhecido e almejado em unidades de conservação marinhas (Roberts et al. 2001). Entretanto, em ambientes de água doce, existe uma clara lacuna de informações, o qual poderia reforçar o papel de UCs de água doce, não só como importante ferramenta de conservação, mas também de aumento de lucros para as comunidades ribeirinhas adjacentes.

As coletas de peixes feitas nos lagos de planície de inundação estiveram mais correlacionadas com fatores ambientais do que com o efeito das UCs. Este resultado é corroborado quando os desembarques pesqueiros oriundos dos lagos são analisados separadamente, os quais mostram valores de CPUE de pescadores similares entre áreas protegidas e desprotegidas. Profundidade e suas variáveis correlacionadas (pH, zona eufótica e condutividade), cobertura de habitat e morfologia do habitat (tamanho e forma) influenciaram a biomassa, riqueza, abundância, tamanho e nível trófico dos peixes. A falta de relação encontrada entre as assembleias de peixe de lagos e as UCs é possivelmente causada pelas diferenças na pressão pesqueira entre o rio e os lagos marginais. Cerca de 67% de todos os peixes capturados pelos pescadores foram originados do canal principal do Rio Tapajós. Dessa forma, os impactos causados pela pesca seriam mais evidentes no canal principal do rio do que nos lagos marginais. Não obstante, o manejo de pequena escala (co-manejo), que ocorre em cinco lagos da região (dois na área não protegida, um na FLONA e dois na RESEX; Hallwass et al., in press), pode ter diminuído os impactos pesqueiros incidentes sobre a assembleia de peixes das áreas protegidas e não protegidas no baixo Tapajós. De qualquer forma, os resultados obtidos nesse trabalho indicam que a variação ambiental entre os lagos de planície de inundação cria diferentes associações de espécies de peixe no espaço e no tempo e portanto essas variáveis devem ser levadas em conta em qualquer plano de manejo na Amazônia.

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