



Seasonal and interannual dynamics of river-floodplain multispecies fisheries in relation to flood pulses in the Lower Amazon

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ABSTRACT

River-floodplain fisheries are highly productive as seasonal water level changes, known as ‘flood pulses,’ increase the productivity of fish populations by providing them with feeding and reproductive opportunities in the floodplains. However, current understanding of flood pulse effects on fisheries activities at seasonal and interannual time scales remains deficient. Here, we analyze a comprehensive dataset of the Lower Amazon region to address the following questions: How flood pulses affect river-floodplain fishing strategies with respect to species composition and habitat? What is the interannual lag of hydrological effects on fisheries yields? And does that lag depend on the life-history strategy of the target fish species? A principal coordinates analysis indicated that fishing activities followed a clear seasonal pattern characterized by alternating habitat and species. Cross-correlation analyses indicated the existence of positive effects caused by mean water levels on fish catches roughly two or three years later. The lag of such water level effects on fish catches was proportional to species longevity, being 22 months for short-lived species with a mean age at catch of 21 months, 26 months for medium-lived species with a mean age at catch of 27.2 months, and 42 months for short-lived species with a mean age at catch of 33.7 months. The results of this study highlight the large seasonal and annual variability of tropical river-floodplain fisheries, and underscore the dependence of fish catches on natural river hydrological cycles. Because these fisheries are suffering increasing exploitation pressures, conservation measures are necessary to protect the hydrology of Amazonian rivers.

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1. Introduction

River-floodplain fisheries are highly productive as seasonal water level changes, known as ‘flood pulses’ (Junk et al., 1989), increase the productivity of fish populations by providing them with key feeding and reproductive opportunities in the floodplains (Bayley, 1995; Welcomme, 1985). Most river-floodplain fisheries occur in tropical and sub-tropical regions, where fish species diversity is high and the human populations depending on fisheries have few livelihood alternatives (Bene et al., 2009; Welcomme et al., 2010). Yet, current understanding of flood pulse effects on the dynamics of fish populations and related fisheries activities remains sparse (Welcomme and Halls, 2004).

Floodplain fish species have developed physiological adaptations, life-history strategies, and reproductive and feeding behaviors to cope with, and take advantage of, flood pulses (Lowe-McConnell, 1975; Welcomme, 1979; Bunn and Arthington, 2002). Flood pulses primarily change the availability of habitats for fish populations. Rising water levels make available grass fields, shrubs, forests, and macrophyte habitats that provide fish with abundant food items and excellent nursery conditions. Intensive feeding during high waters permit fish to build fat reserves that support them during low waters, when food is scarce and they have to develop their gonads for spawning early during high waters (Poulsen et al., 2004).

The migratory behavior of fish in floodplains appears to be closely linked to reproduction and changes in river water levels (Bunn and Arthington, 2002). Many fish species migrate laterally from floodplain lakes or river channels onto vegetated floodplain habitats and stay there until water levels are maxima or receding waters force them to migrate back to river channels or floodplain

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lakes (Cox Fernandes, 1997; Castello, 2008a,b; Arantes et al., 2013). In floodplain lakes, fish often suffer high natural mortality rates during low waters due to high temperatures and/or low oxygen levels (Junk et al., 1983; Welcomme, 1985; Matthews and Marsh-Matthews, 2003). Many species return to river channels at this time, and some of them migrate longitudinally upstream, often hundreds or even thousands of kilometers to spawn or search for new habitat (Ribeiro and Petrere, 1990; Goulding, 1980). These seasonal changes in water levels and fish habitat affect the catchability of fishing gear. Most gear generally possess low catchability rates during high waters due to great expansions in flooded area, and high catchability rates during low waters as fish are concentrated in floodplain lakes or are caught in migratory schools when they migrate out of the floodplains or upstream in river channels (Halls and Welcomme, 2004).

Interannual variations in flood pulses can affect fish recruitment, growth, and mortality, thereby causing changes in fish biomass available for harvesting (Welcomme and Halls, 2004; Bailly et al., 2008). Years with intense high waters generally offer more feeding opportunities, increasing fish biomass available for harvesting in near-future years. Conversely, intense low water years can reduce fish biomass through increased natural or fishing mortality (Welcomme, 1985). As such, previous studies have found correlations between high or low water intensity in one year and fisheries catches in later years in Africa (e.g. Welcomme, 1979, 1985; Moses, 1987; Laë 1992, 1995) and the Amazon (de Mérona and Gascuel, 1993; Castello et al., 2015). Fisheries dynamics in river-floodplains is thus controlled by seasonal and interannual variability in water levels.

However, most studies on multispecies river-floodplain fisheries have focused on seasonal variability in overall fish catches, seasonal fishing patterns of a few target species, or the year-round species composition of the fish catch (e.g. Batista et al., 1998; Craig et al., 2004; Vallejos et al., 2013). To our knowledge, no study has investigated how flood pulses affect fishing strategies with respect to species composition, habitat, and seasonal effects. Several opportunities for fishing exist in tropical river-floodplains, as fish populations exhibit a diversity of life-history strategies and habitat availability varies geographically and temporally following the seasonal rise and decline of water levels. Furthermore, although previous studies have identified interannual flood pulse influences on fish catches, to date only a few studies have systematically quantified the lag between flood pulses and fishery yields. Flood pulse influences on fishery yields can be expected to mainly act on spawning and recruitment success (Freitas et al., 2012), because environmental processes occurring during the early life stages generally have profound influences on fish population dynamics (Fuiman and Werner, 2002). The effects of such phenomena should be noticeable in fishery catches after the time it takes for fish eggs and larvae to recruit to the fishery. Two- and three-year flood pulse lags affected fishery catches of all species together in the Central and Lower Amazon Basin regions, and similar lags were found for fish catches grouped in feeding groups in the Lower Amazon (de Mérona and Gascuel, 1993; Castello et al., 2015). This sort of lag of flood pulse influences on fishery yields is expected to depend on the life history and mean age at catch of the targeted species. Such lags are expected to be greater for large-sized species with slow growth, late maturation, and long life-span (i.e., K-strategists) than for small-sized species with high growth and mortality rates, early maturation, and short life-span (i.e., r-strategists).

Fisheries management requires improved understanding of seasonal and interannual variability in river-floodplain fisheries, particularly as a generalized paucity of data has impeded advances on the topic. These fisheries are suffering increasing exploitation pressure and the hydrology of the ecosystems that sustain them is becoming increasingly altered by dam construction and land

cover changes (Welcomme et al., 2010). The effects of altered flow regimes on tropical aquatic fishes are predicted to be stronger than those caused by changes in temperature induced by climate change (Meisner, 1992; Poff et al., 2001). These effects will be species-specific (Ficke et al., 2007), so they will depend on the life-history strategies of the species involved.

Here, we analyze a comprehensive dataset on multispecies fisheries of the Lower Amazon region to examine how hydrological variability affect populations of fish species with different life-history traits and how such effects impact fishing activities. We address the following research questions: (1) How flood pulses affect river-floodplain fishing strategies with respect to species composition and habitat? (2) What is the interannual lag of hydrological effects on fisheries yields? And (3), does the lag of hydrological effects on fishery yields depend on longevity and mean age at catch of the target fish species?

2. Methods

2.1. Study area

This study was done based on data collected from the fishing fleet of the Lower Amazon region (Isaac et al., 2008), in a 550 km stretch of the Amazon river-floodplains, between the cities of Almeirim, State of Pará, and Parintins, State of Amazonas, Brazil (Fig. 1). The ecosystem is classified as *várzea*, which are river-floodplains influenced by nutrient- and sediment-rich waters stemming from the Andes Mountains in the Amazon Basin (Sioli, 1968). Fishing occurs in a variety of habitats, including river channels, which are the deepest habitats, and a series of progressively shallower habitats in the floodplains, including connecting channels, lakes, herbaceous fields, shrubs, and forests (Hess et al., 2003). These habitats are seasonally inundated by flood pulses of 6.2 m on average in amplitude, with a maximum water level in May-June and a minimum in October (Fig. 2a). Fisheries in the study area sustain per capita fish consumption rates of 40–94 kg yr⁻¹, well above the global average of 16 kg yr⁻¹ (Isaac and Almeida, 2011).

2.2. Data collection

The fisheries data were collected between January 1993 and December 2004 in nine cities (Fig. 1) through daily interviews (Monday-Saturday) conducted with boat masters or the fishers themselves at the moment of landing. Data collected for each fishing trip included vessel type (wooded motorized boat or wooded canoe, with average 11 m length), number of fishers, number of days spent fishing, fishing gear used, habitat of fishing (i.e. floodplain lake or river channel), and total catch in weight for each species. Fish species were identified by their local common names, some of which encompass groups of species (Table 1). Respective daily river water level data measured at Óbidos (Fig. 1) was obtained from ANA (2015).

2.3. Data analyses

The original dataset included fishing trips in which a variety of fishing gears and vessel types and sizes were employed. The data were filtered to include only fishing trips made by motorized boats using gillnets to reduce variance caused by different catchability rates among different vessel and gear types. The resulting data of fishing trips made by motorized boats using gillnets included 54,798 fishing trip records that contributed with 52% of total fisheries catches during the study period. Catch (kg) and fishing effort (number of fishers × days spent fishing) were calculated for every fishing trip and summed per month to create a balanced sample design. Because the variance of catch increased with effort, catch

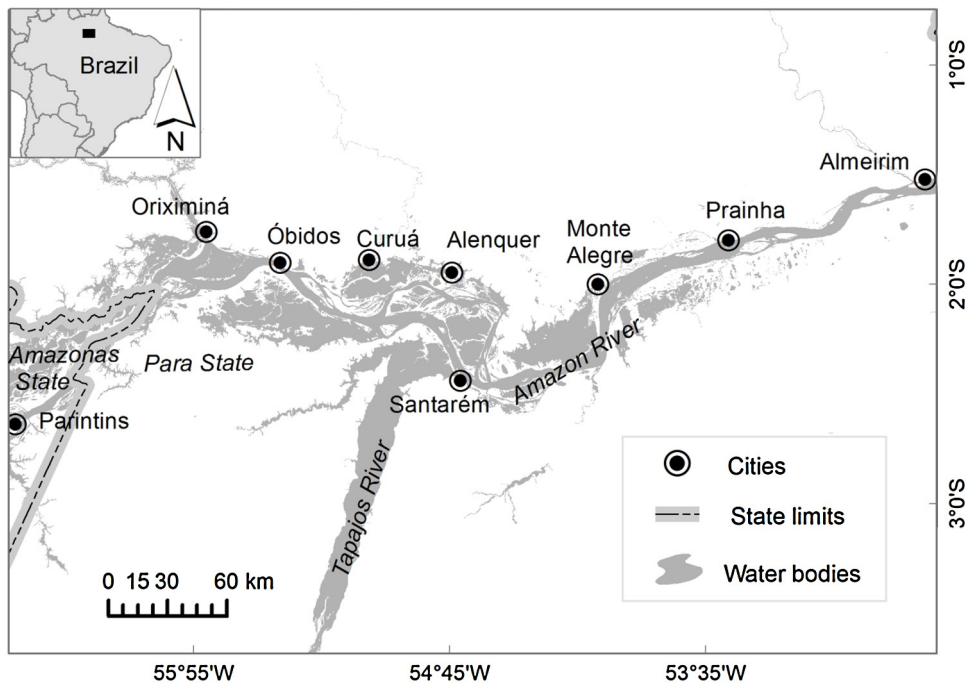


Fig. 1. Map of the Lower Amazon region near the municipalities of Santarém, State of Pará, Brazil.

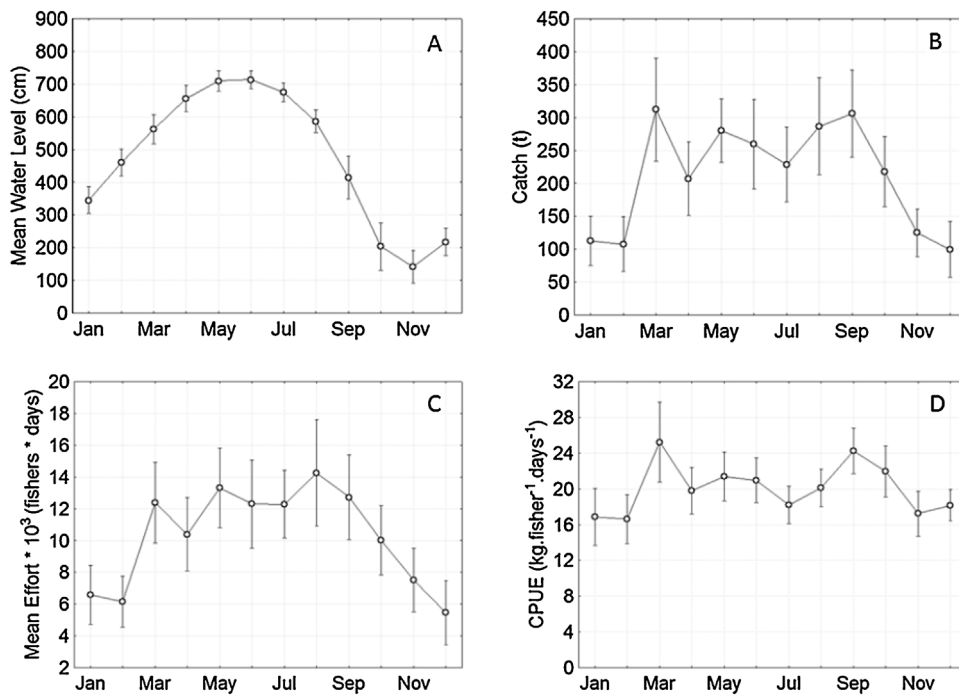


Fig. 2. (A) Mean monthly water levels in Óbidos and respective confidence interval (95%). (B) Monthly average for catch. (C) Monthly effort, and (D) respective average catch per unit effort (CPUE) for the study period.

per unit effort (CPUE) for every month was estimated by dividing monthly catch by monthly effort (Petreere et al., 2010).

To understand how flood pulses affect fishing strategies with respect to species composition and habitat, an unconstrained ordination based on Principal Coordinates Analysis (PCO) was used to visualize similarities in monthly CPUE. The data were transformed by fourth roots and grouped based on the Bray Curtis distance for all 43 fish species regularly caught. The percentages of the explained variance in the first two axes were used to evaluate the impor-

tance of these axes. The Spearman correlation coefficient for each individual species within each of the canonical axes was calculated to understand species composition in the ordination. Species with correlations greater than 0.6 were shown graphically as a vector. The effects of habitat (river channels and floodplain lakes) and month of fishing on the species composition of catch were investigated using factor labels on the data. A PERMANOVA and a pairwise comparison were used to identify treatment groups that differed.

Table 1

Fish species, average catch contribution (during the study period), best available information on longevity from Isaac et al. (2012), and respective longevity group.

Common Name	Scientific name	Family	Order	Catch (%)	T _{max}	Longevity Group
Mapará	<i>Hypophthalmus edentatus</i> , <i>H. marginatus</i>	Pimelodidae	Siluriformes	35	8	Medium-lived
Dourada	<i>Brachyplatystoma rousseauxii</i>	Pimelodidae	Siluriformes	9	11	Long-lived
Curimata	<i>Prochilodus nigricans</i>	Prochilodontidae	Characiformes	9	6	Short-lived
Acari	<i>Squaliforma emarginata</i> , <i>Pterygoplichthys pardalis</i>	Loricariidae	Siluriformes	5	6	Short-lived
Fura Calça	<i>Pimelodina flavipinnis</i>	Pimelodidae	Siluriformes	5	6	Short-lived
Jaraqui	<i>Semaprochilodus taeniurus</i> , <i>S. insignis</i>	Prochilodontidae	Characiformes	5	7	Medium-lived
Pescada Branca	<i>Plagioscion squamosissimus</i> ; <i>P. surinamensis</i>	Scianidae	Perciformes	5	10	Medium-lived
Surubim	<i>Pseudoplatystoma fasciatum</i> , <i>P. tigrinum</i>	Pimelodidae	Siluriformes	4	18	Long-lived
Aracu/Piau	<i>Schizodon fasciatus</i> , <i>S. vittatus</i> , <i>Leporinus</i> spp, <i>Rhytiodus argenteofuscus</i> , <i>Laemolita taeniata</i>	Anostomidae	Characiformes	3	8	Medium-lived
Tambaqui	<i>Colossoma macropomum</i>	Serrasalmidae	Characiformes	3	13	Long-lived
Pacu	<i>Metynnis</i> spp, <i>Mylossoma duriventre</i> , <i>M. aureum</i>	Serrasalmidae	Characiformes	2	4	Short-lived
Filhote	<i>Brachyplatystoma filamentosum</i>	Pimelodidae	Siluriformes	2	14	Long-lived
Piramutaba	<i>Brachyplatystoma vaillantii</i>	Pimelodidae	Siluriformes	2	22	Long-lived
Acara	<i>Astronotus crassipinnis</i> , <i>Geophagus proximus</i>	Cichlidae	Perciformes	1	3	Short-lived
Tucunaré	<i>Cichla monoculus</i> , <i>Cichla</i> sp.	Cichlidae	Perciformes	1	7	Medium-lived
Matrinxa/Piabanha	<i>Brycon</i> spp	Bryconidae	Characiformes	1	6	Short-lived
Apapa	<i>Pellona flavipinnis</i> , <i>P. castelnaeana</i>	Pristigasteridae	Clupeiformes	1	8	Medium-lived
Pirapitinga	<i>Piaractus brachypomus</i>	Serrasalmidae	Characiformes	1	7	Medium-lived
Cujuba	<i>Oxydoras niger</i>	Doradidae	Siluriformes	1	14	Long-lived
Arraia	<i>Potamotrygon motoro</i> , <i>Potamotrygon</i> sp.	Potamotrygonidae	Myliobatiformes	<1	–	–
Branquinha	<i>Curimata</i> spp, <i>Cyphocharax</i> spp, <i>Psectrogaster</i> spp, <i>Curimatella</i> spp, <i>Potamorhina latior</i> , <i>P. altamazonica</i>	Curimatidae	Characiformes	<1	–	–
Cara de Gato	<i>Platynematachthys notatus</i>	Pimelodidae	Siluriformes	<1	–	–
Jandia	<i>Leiarius marmoratus</i>	Pimelodidae	Siluriformes	<1	–	–
Jeju	<i>Hoplerythrinus unitaeniatus</i>	Erythrinidae	Characiformes	<1	–	–
Mandi	<i>Pimelodus blochii</i>	Pimelodidae	Siluriformes	<1	–	–
Mandube	<i>Ageneiosus inermis</i>	Auchenipteridae	Siluriformes	<1	–	–
Peixe-Cachorro	<i>Hydrolycus scomberoides</i>	Cynodontidae	Characiformes	<1	–	–
Piracatinga	<i>Calophysus macropterus</i>	Pimelodidae	Siluriformes	<1	–	–
Piranha	<i>Pygocentrus nattereri</i> , <i>Pristobrycon</i> spp, <i>Serrasalmus</i> spp	Serrasalmidae	Characiformes	<1	–	–
Pirarucu	<i>Arapaima</i> spp	Arapaimidae	Osteoglossiformes	<1	–	–
Poraque	<i>Electrophorus electricus</i>	Gymnotidae	Gymnotiformes	<1	–	–
Saranha/Cachorra	<i>Cynodon gibbu</i> , <i>Rhaphiodon vulpinus</i>	Cynodontidae	Characiformes	<1	–	–
Sardinha	<i>Tripottheus</i> spp	Tripottheidae	Characiformes	<1	–	–
Tamoata	<i>Hoplosternum littorale</i>	Callichthyidae	Siluriformes	<1	–	–
Traira	<i>Hoplias malabaricus</i>	Erythrinidae	Characiformes	<1	–	–
Charuto/Erana	<i>Bivibranchia</i> sp, <i>Hemiodus</i> spp, <i>Anodus elongatus</i>	Hemiodontidae	Characiformes	<1	4	Short-lived
Aruana	<i>Osteoglossum bicirrhosum</i>	Osteoglossidae	Osteoglossiformes	<1	10	Medium-lived
Bacu	<i>Pterodoras granulatus</i> , <i>Lithodoras dorsalis</i>	Doradidae	Siluriformes	<1	14	Long-lived
Barbado	<i>Brachyplatystoma platynemum</i>	Pimelodidae	Siluriformes	<1	14	Long-lived
Jau	<i>Zungaro zungaro</i>	Pimelodidae	Siluriformes	<1	17	Long-lived
Pirarara	<i>Phractocephalus hemiliopterus</i>	Pimelodidae	Siluriformes	<1	14	Long-lived
Piranambu	<i>Pinirampus pirinampu</i>	Pimelodidae	Siluriformes	<1	–	–

Analyses were done in Primer Software 6.0 (Clarke and Gorley, 2006).

To quantify the lag effects of interannual variations in hydrology (i.e., anomalous wet and dry years) on fisheries yields, cross-correlation analysis was employed. Cross-correlation is a commonly used method for searching patterns or signals in time series of fishery data (i.e. Fogarty, 1998; Borges et al., 2003; Moraes et al., 2012); it estimates the degree to which two series are correlated as a function of the lag of one relative to the other (Chatfield, 2004). The catch data matrices necessary to perform cross-correlation analysis were developed based on results of the PCO analysis, which allowed creating three groups for the 25 main species (comprising 99% of the catch in weight, Table 1) based on habitat, season, and longevity of the species harvested. The three groups described in Table 1 were: long-, medium-, and short-lived species. Habitat and season were selected as the criteria

for creating three species groups because together they describe fishing activities with relatively homogeneous characteristics (e.g., large catfishes harvested during low waters in river channels). Mean longevity was estimated for each of the three species groups (long-, medium-, and short-lived species) and for all 25 species grouped together using data from Isaac et al. (2012). Species-specific longevity estimates were weighed by contribution to total catch in weight for each group. Longevity was selected as a criterion to understand effects of flood pulse anomalies because it is expected to be proportional to age at catch for most species in the study area. Longevity is inversely correlated with mortality (Holt, 1965), and mortality rates are related to mean size (or mean age) of individuals in the catch (Beverton and Holt, 1956).

Anomalies in monthly catch, effort, and water levels for all groups of long-, medium-, and short-lived species, as well as all 25 species together, were computed to eliminate the large intra-

annual harmonic changes that tend to hide year-to-year variations in time series with strong seasonality (e.g. McInnes and Broenkow, 1978). Anomalies in the data were computed by dividing the differences between each month's data and the respective historical average by the respective standard deviation. Simple linear regressions were computed between the monthly anomalies of catch and effort for all species together (total catch) and for each of the tree longevity groups. The residuals of these resulting regressions (response variable) were tested for cross-correlations with the anomalies of monthly water levels (explanatory variable) for preceding months, allowing identification of the strongest correlations among lags from one to up to 48 months. Up to 48 months lags were considered because they encompass most of the range of mean ages at catch found in Amazonian fisheries (Isaac et al., 2012). The strength of correlations for month with lag 0 was also assessed due to potential immediate effects of variability of monthly water levels on catchability rates. The significance of each lag were evaluated using a t -test with $n-2$ ° of freedom, where n is the number of samples that overlap (Legendre and Legendre, 1998). All analyses used Type I error $\alpha = 5\%$. Cross-correlation analyses were done using PAST Software (Hammer et al., 2001).

To understand if the lags depend on the longevity of the target fish species, the lags identified in the cross-correlation analyses were compared across all longevity groups. An ancillary analysis compared the lags identified to the mean age at catch of a few selected species for which data were available for the study area (Castello et al., 2011). Mean age at catch was estimated based on mean length at catch and on the von Bertalanffy growth parameter estimates summarized in Isaac et al. (2012).

3. Results

The PCO analysis indicated that fishing activities follow a clear seasonal pattern of alternating habitat and species. Both habitat (Pseudo $F=86.81$; $p=0.001$) and month (Pseudo $F=10.24$; $p=0.001$) were significant factors, as well as the interaction (Pseudo $F=2.22$; $p=0.001$). The first two axes of the PCO explained almost 40% of total variation in the data (Fig. 3). The seasonal flooding cycle depicted in Fig. 3 followed an anticlockwise order of species harvest. *Hypophthalmus* spp. and *P. flavipinnis* were targeted in March–April during rising waters in floodplain lakes, followed by migratory *Semaprochilodus* spp., which were targeted in May–June in river channels when water levels were maxima. Long-distance migratory *Brachyplatystoma rousseauxii*, *B. filamentosum*, *B. platyneum* and *Zungaro zungaro* were targeted in August during declining waters in river channels. Migratory *Pseudoplatystoma* spp. and *Phractocephalus hemiliopterus* were targeted between September–December in river channels, as were the non-migratory *Cichla* spp., *Osteoglossum bicirrhosum*, *Oxidoras niger*, and other small Cichlidae species during the same period in floodplain lakes. Non-migratory *P. squamosissimus* were targeted in December–January in floodplain lakes.

The observed patterns in fishing activity across fish species and habitats (Fig. 3) produced an eight month period of large catches formed by three smaller peaks in catches during rising, high, and declining water levels (Fig. 2a, b). These three peaks in catch were caused by increases in CPUE, which led to increases in fishing effort (Fig. 2a–d) for *Hypophthalmus* spp in March–April, *Semaprochilodus* spp in May–June, and long-distance migratory catfish (as *B. rousseauxii*) in August (Figs. 2b–d and 3). Mean monthly catch and effort were 212 t and 10,280 fishers × days, respectively, while mean monthly CPUE was 20 kg fisher⁻¹ days⁻¹. The coefficients of variation of monthly catch and effort during the study period were 55% and 45%, respectively, while that of CPUE was only 25%.

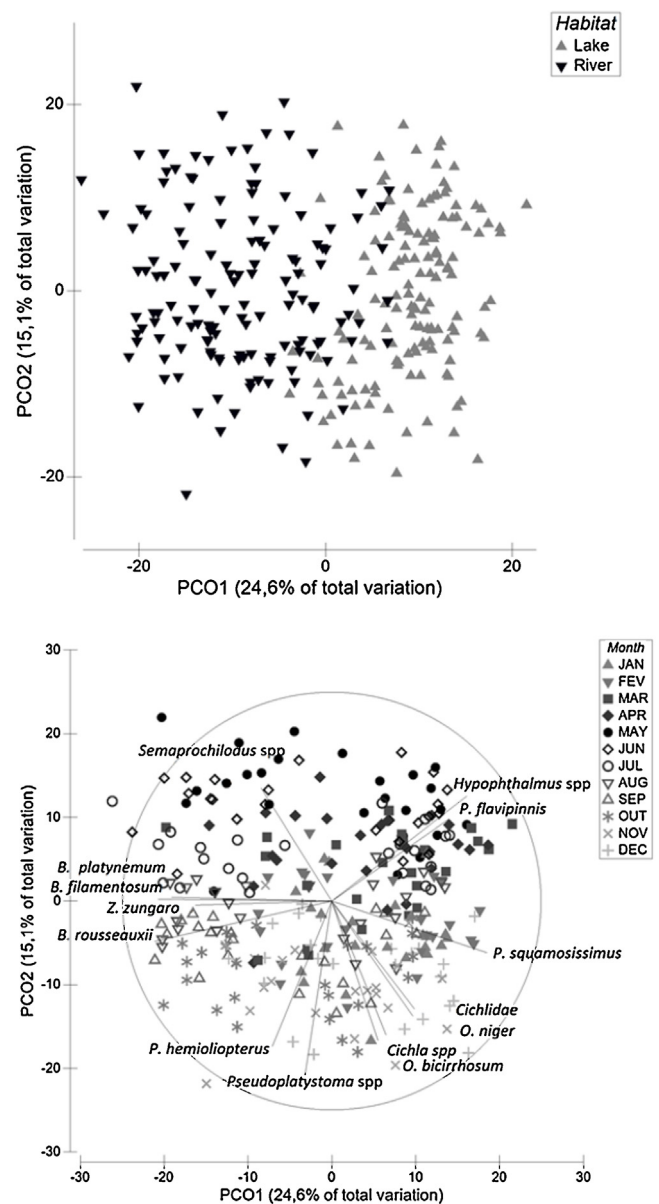


Fig. 3. Principal coordinate analysis ordination (PCO) of the 43 most important fish species caught during the year, including habitat and month of capture. Selected species in vectors have high correlation (>0.6) with first two axes.

The PCO results (Fig. 3) in light of longevity estimates (Table 1) indicated the presence of three main species groups. The most distinguished group was comprised mainly of long-lived, large-bodied, catfish species that were harvested during their upstream migrations in river channels during low waters. The second group was comprised of generally shorter-lived species possessing small- to medium-sized bodies that were harvested in both floodplain lakes and river channels mainly during rising and high waters. The broad range of life cycles included in this second group required dividing it in two groups (here forth referred to as 'short-' and 'medium-' lived species) to better understand flood pulse lag effects in relation to longevity.

The cross-correlation analyses indicated the existence of positive effects between monthly water levels in one year and fish catches roughly two or three years later (Table 2). Cross-correlations analyses of all species together indicated that the lag of hydrological influence on fishery catches was of 22 months (Table 2). The lags of the three groups identified by the PCO anal-

Table 2

Results of the regressions analysis of the catch on fishing effort (anomalies) and results of the cross-correlation analysis of the residuals of the catch on the anomalies of water level.

Longevity Group	Catch * Effort (anomalies)				Lag 0 Correlation		Lag 1–48 Correlation		
	a	b	r	p	r	p	Lag	r	p
Short-lived	0.000	0.006	0.87	0.0000	0.01	0.8825	22	0.32	0.0003
Medium-lived	0.001	0.816	0.82	0.0000	0.11	0.2056	26	0.27	0.0027
Long-lived	0.035	0.893	0.79	0.0000	−0.25	0.0019	42	0.27	0.0055
Total	0.000	0.886	0.89	0.0000	−0.05	0.5062	22	0.45	0.0000

ysis were roughly proportional to the longevity of the involved species: 22 months for short-lived species, 27 months for medium-lived species, and 42 months for long-lived species (Table 2). These monthly lags were always accompanied by strong (though weaker) lags in the months before and after them, so the observed effects in catch occurred not only during one month but rather over six to seven month periods (e.g., periods of high and low waters). Catches of all species and short- and medium-lived species were not correlated to Lag 0, but catches of long-lived species were (Table 2), indicating that water level anomalies in the month in which fishing took place did not affect gear catchability of the former three groups, but did affect that of the latter group. Low waters allowed high yields of long-lived species, probably through increased catchability rates in river channels.

The lag of water level effects on fish catches was close and proportional to mean age at catch of the species in the short- and medium-lived groups and total catch, but it was a bit longer than mean age at catch estimated for long-lived species. Mean age at catch was 21 months for short-lived species, 27 months for medium-lived, and 34 months for long-lived (Table 3). Mean age at catch for all species together was 28 months.

4. Discussion

4.1. Seasonal effects

The results of this study document the large seasonal and interannual variability of tropical river-floodplain fisheries. The seasonality of flood pulses allowed fishers to exploit 43 species in river channel and floodplain habitats over the course of the year, though the catch was dominated by a few species. Because flood pulses dramatically alter mean fish densities and associated gear catchability, Amazonian fishers appear to have developed three main fishing strategies to minimize seasonal variability in CPUE (Fig. 2). Fishers target fishes in floodplain lakes during rising waters (e.g., *Hypoththalmus* spp), characiform fishes migrating out of the floodplains during high and declining waters (e.g. *Semaprochilodus* spp.), and migratory catfishes migrating upstream in river channels during declining and low waters (e.g., *B. rouseauxii*; Fig. 3). Nevertheless, there was a low in total catch during low waters (November–February), which was partly due to closed seasons for most species (December 15–March 15; Fig. 2).

4.2. Interannual effects

Seasonal variability in the availability of exploitable fish biomass is exacerbated by variability in fish biomass caused by interannual variability in flood pulses. In the study area, the intensity of low waters in any given year was negatively related to total (multi-species) catch two years later (Castello et al., 2015). Similarly, in the Central Amazon fish biomass in a given year (as denoted by CPUE) was negatively related to low waters two years prior (de Mérona and Gascuel, 1993).

The positive effect of water levels with a lag of 22 months, though slightly under the estimated mean age at catch of 27.8

months (Table 3), is consistent with other studies showing that Amazonian fisheries are under lower exploitation pressure than their African or European counterparts, where the lag of water level effects on fish catches is usually of around one year (Welcomme, 1985). For example, in the Danube basin, the intensity of high waters lead to increased fish catches one year later (Chitravadivelu, 1974). As fishing pressure increases in tropical multispecies fisheries, the average body length and age at recruitment into the fishery decreases via depletion of the larger-sized species that are generally targeted. This process of change of the exploited fish assemblage follows the ‘fishing down’ process of Welcomme (1999), which is not to be confounded with the ‘fishing down marine food webs’ concept of Pauly et al. (1998) by which fishing pressure decreases mean trophic level of the catch. The lag effect of 22 month documented here serves as a management point of reference to evaluate the status of the studied fishery in future years.

A positive correlation between water levels in any given month and catch 22 months later can be explained via processes of decreased natural mortality and increased recruitment and body growth, which are generally associated with increased availability of water in the system. Low waters generally decrease water quality (i.e. high temperatures, low oxygen levels) and intensify biotic interactions in floodplain lakes, causing high natural mortality (Matthews and Marsh-Matthews, 2003). Conversely, high waters generally foster feeding and survival rates of fish of all ages, including larvae and young-of-the-year, as fish find more feeding and nursery opportunities in floodplain habitats (Goulding, 1980; Lobón-Cerviá et al., 2015). As such, the results indicate that “dry” years lead to decreased catches, and “wet” years lead to increased catches 22 months later.

That the lag of water level effects on fish catches was close and roughly proportional to mean age at catch for short- and medium-lived species and total catch suggests that flood pulse effects on fish population biomass available for harvesting act mainly on early life stages. Environmental influences on early life stages have been shown to strongly influence fish population dynamics in a variety of ecosystem types across the globe (Fuiman and Werner, 2002).

However, catches of long-lived species responded to water level anomalies in a slightly different fashion. Water levels during the month when fishing took place affected the catch of long-lived species in an inverse manner, probably by making these species more vulnerable to fishing gear. As these species were harvested during low water, water levels lower than normal appeared to increase the efficiency of gillnets. Furthermore, the lag of water level effects on catches of long-lived species was longer than the estimated mean age at catch by about nine months. There are several possible explanations for this finding, as the complex life cycles of these species remain poorly understood. The mean age at catch of this species group could be longer than that estimated here, which was based on only a few species for which data were available. The growth parameters of these species were estimated based on length-based methods, but such methods are known to produce under-estimates of growth rates for long-lived species, because old fishes are difficult to sample (Isaac, 1990). Additionally, water

Table 3
Estimated mean total length at catch, von-Bertalanffy growth equation parameters, and mean age at catch of key species composing each longevity group, for the study area from Isaac et al. (2012) and Castello et al. (2011). Mean group age at catch is weighted by the catch contribution (Table 1) of each species. Mean group age at catch was estimated only on the presented species, because those are the only species for which estimates of mean length at catch in the study area exist.

Species groups		Length at catch (cm)	L-inf	K	Age at catch (months)	Mean group age at catch (months)
Short-lived	Curimatá	34	63	0.48	19.7	21
	Acari	31	50	0.5	23.2	
Medium-lived	Mapará	40	69.5	0.38	27.1	27.2
	Jaraqui	23.5	35.5	0.5	26	
	Pescada	35	68.4	0.3	28.7	
Long-lived	Dourada	90	140	0.33	37.4	33.7
	Surubim	87	178	0.31	33.6	
	Tambaqui	43	119	0.22	24.5	
	Filhote	97	240	0.2	31.1	
Total						27.8

levels could positively influence the spawners of these long-lived species via increased individual weights before their spawning. Water levels could also influence the dynamics of their populations in different ways from the other species. Unlike the short- and medium-lived species, some long-lived species (e.g. *B. vaillanti*) are thought to spawn in the upper reaches and utilize estuarine (Barthem and Goulding, 1997) and headwater areas (Hegg et al., 2015) as nursery zones. So they do not depend directly on the floodplains for reproduction and recruitment, though they do depend on floodplain prey fishes. Because most of these long-lived species are fished intensely (Barthem and Petrere, 1995; Isaac and Ruffino, 1999; Petrere et al., 2004; Alonso and Pirker, 2005; Castello et al., 2011, 2013), additional studies are needed to elucidate flood pulse effects on their complex population dynamics.

4.3. Implications

The results of this study underscore the influence of the hydrological cycle on fisheries strategies of tropical river-floodplain ecosystems. An intricate schedule of alternating habitats and species maintain relatively high fisheries productivity for fishers for most of the year, optimizing their economic returns and providing fish protein for local populations. At the same time, variability across years in hydrological cycles affects natural and fishing mortality, recruitment, and body growth of the exploited fishes, affecting fish biomass available for harvesting in a manner that depends on the longevity and age at catch of the species involved.

River hydrological alterations caused by construction of dams, land cover change (e.g., deforestation), and climate change affect the seasonal and annual dynamics of these fisheries. The Lower Amazon is susceptible to hydrological alterations occurring in most of the basin and it has suffered historical degradation of floodplain habitats via floodplain deforestation (Renó et al., 2011). This vulnerability is intensifying as hydrological alterations mark the next phase in Amazonian development and many economic strategies target riverine ecosystems (Isaac et al., 1998; Raffles and Wiklerprins, 2003).

Available predictions of the impact of ongoing human activities on the hydrology of the Amazon mainstream indicate that, if current trends continue, the magnitude of high water will decrease and the frequency and severity of low water events in the basin will increase (Castello and Macedo, 2016; Coe et al., 2009; Mahli et al., 2007). Decreased high water events are expected to decrease fish growth and recruitment processes, and more frequent and intense droughts are expected to intensify natural mortality rates, disrupting the observed seasonal fisheries dynamics and decreasing total fish catches. In the short-term, catches of long-lived catfish species could increase, but they would be expected to inevitably decrease in the long-term. Such impacts on fish populations would be expected to synergize with ongoing impacts due to floodplain deforestation

and overfishing, undermining one of the principal food and employment sources in the region. Plans for the protection of the natural hydrology of Amazonian rivers are necessary to avoid the degradation of these important fisheries.

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