Flood pulse influences on exploited fish populations of the Central Amazon

Jesse E. B. Olsen

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Leandro Castello, Chair
Yan Jiao
Donald J. Orth

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Public Abstract

Seasonally fluctuating water levels, known as flood pulses, influence the population dynamics and catches of fishes from river-floodplains. Although different measures of flood pulses, here called flood pulse variables, have been related to changes in catches of river-floodplain fishes, the flood pulse variables that have the strongest relationships to catches have not been identified. Furthermore, it is unclear if flood pulses influence catches of river-floodplain fishes with different life history strategies in different ways. Catches of 21 taxa from approximately 18,000 fishing trips were modeled as a function of fishing effort, gear type, seasonal flood pulse variables, and interannual flood pulse variables. These models were analyzed to understand which flood pulse variables had the strongest relationships to catches, and evaluate different flood pulse influences among taxa with different life history strategies. High water flood pulse variables generally had positive influences on catches in future years, while low water flood pulse variables generally had negative influences on catches in future years. Flood pulses generally had stronger influences on the catches of fishes that produce many smaller eggs than on catches of fishes that produce fewer and larger eggs. Variation was observed in strengths and types of flood pulse influences on catches of fishes with similar and different life history strategies. While my results were generally consistent with prevailing knowledge of how flood pulses influence catches of fishes, other biological factors of specific fish populations may further explain population responses to flood pulses.

Academic Abstract

Seasonally fluctuating water levels, known as flood pulses, influence the population dynamics and catches of fishes from river-floodplains. Although different measures of flood pulses, here called flood pulse variables, have been correlated to changes in catches of river-floodplain fishes, the flood pulse variables that have the strongest relationships to catches have not been identified. Furthermore, it is unclear if flood pulses influence catches of river-floodplain fishes with different life history strategies in different ways. Catches of 21 taxa from approximately 18,000 fishing trips were modeled as a function of fishing effort, gear type, seasonal flood pulse variables, and interannual flood pulse variables. These models were analyzed to understand which flood pulse variables had the strongest relationships to catches, and evaluate different flood pulse influences among taxa with different life history strategies. High water flood pulse variables generally had positive influences on catches in future years, while low water flood pulse variables generally had negative influences on catches in future years. Flood pulses generally had stronger influences on the catches of fishes with high fecundities and smaller eggs than on catches of fishes with low fecundities and larger eggs. Variation was observed in strengths and directions of flood pulse influences on catches of fishes with similar and different life history strategies. While my results were generally consistent with prevailing knowledge of how flood pulses influence catches of fishes, other biological factors of specific fish populations may further explain population responses to flood pulses.

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Preface

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Chapter 1: Introduction

Seasonally fluctuating river water levels, known as flood pulses, support highly productive ecosystems and large fish populations (Junk et al. 1989, Tockner et al. 2000). The fluctuation between high and low water levels in river-floodplain ecosystems transfers nutrients between aquatic and terrestrial systems (Junk et al. 1989). Rising water levels and overbank flooding create aquatic habitats on the floodplain and connect previously isolated floodplain lakes. Nutrients mobilized by erosion and allochthonous inputs enhance aquatic productivity on the floodplain, facilitating the growth of phytoplankton, periphyton, and macrophytes. These increases in primary production during high water levels provide food sources for many fish species (Lewis et al. 2001). When flood waters recede, the floodplains enter a seasonal low water period and terrestrial organisms recolonize previously flooded areas. The seasonally fluctuating discharge in river-floodplains creates a network of braided channels and habitats that are transient and spatially diverse. River-floodplain ecosystems are generally more productive and support a greater diversity of organisms than in modified river-floodplains (Bayley 1991, Tockner and Stanford 2002, Alho et al. 2015). River-floodplains in the Amazon Basin support an unrivaled variety of endemic birds, reptiles, amphibians, mammals, and fish species (Alho et al. 2015). However, land use changes and hydrologic alterations threaten the very fabric that makes river-floodplain ecosystems and fish populations so productive (Palmer et al. 2005, Ziv et al. 2012, Alho et al. 2015). Given that the natural hydrology of many river-floodplains has been modified (Rosenberg et al. 2000), understanding how flood pulses influence fish populations is important for efforts to manage the hydrology of modified rivers to balance ecosystem productivity with other river-floodplain services (Bernhardt et al. 2005, Palmer et al. 2005, Ziv et al. 2012).

The changing nature and diversity of aquatic floodplain habitats requires fishes to be able to capitalize on reproductive conditions when they are favorable, and endure unfavorable environmental conditions. As a result, fishes have developed strategies in the form of morphological, physiological, and behavioral adaptations to efficiently utilize the resources in their environments. These strategies that maximize individual longevity have been dubbed life history strategies (Stearns 1992), and may influence how fishes respond to flood pulses (Winemiller 2005, Zeug and Winemiller 2007).

Seasonal flood pulse processes tend to alter the efficiency of fishing gears (Merona and Gascuel 1993, Karenge and Kolding 1995). When water levels rise, gear catchability generally decreases as fish disperse onto the floodplain. During rising water levels, passive gears such as gill nets are generally used when vegetation obstructs the efficient use of active gears such as seines (Bayley and Herendeen 2000). When water levels begin to fall and fish migrate from floodplain habitats to more permanent water bodies, fishers can target large schools of fish using active gears such as seines, cast nets, and dip nets (Almedia et al. 2003, Batista and Petrere 2003). Fishing pressure and catchability are generally the highest during these seasonal migrations (Batista and Petrere 2003). Other specialized gears are also used to target specific taxa with unique ecology, such as the harpoons used to target *Arapaima spp.* during air-breathing events or the gaffs used to target migratory catfish as they navigate rapids in the Madeira River (Goulding 1980).

Flood pulses are thought to influence catches of ecologically diverse fishes in different ways. Many flood pulse variables, defined as characteristics of a hydrologic regime (e.g. maximum stage height, duration of season, rate of water level rise), have been shown to influence fish populations and catches in different ways (Kapetsky 1974, Welcomme and

Hagborg 1977, Halls and Welcomme 2004). High water levels in a given year are generally related to increases in catches in future years, while low water levels in a given year are generally related to decreases in catches in future years (Welcomme and Hagborg 1977). These flood pulse influences are thought to be directly related to the growth and survival of juvenile fishes (Lagler et al. 1971), and generally influence catches after the time it takes for fishes to mature and become recruited to the fishery (Merona and Gascuel 1993, Karenge and Kolding 1995, Chifamba 2000). Flood pulses can also have different influences on fishes with different life history strategies (King et al. 2003, Zeug and Winemiller 2007). High water levels can have stronger effects on the reproductive success of fishes that produce many smaller eggs, compared to fishes that produce fewer and larger eggs (Gorski et al. 2011).

Fish populations in river-floodplains globally face pressure from the negative influences of anthropogenic hydrologic alterations (Davidson et al. 2012, Castello et al. 2013, Alho et al. 2015). Land use changes threaten the connectivity of river channels and floodplains that make river-floodplain ecosystems so productive (Foley et al. 2007, Coe et al. 2009). The damming of rivers for power generation has altered the natural hydrology of rivers (Pringle et al. 2000, Graf 2006), and restricted the seasonal spawning migrations of many fish populations (Larinier 2001). Long-term climate change is predicted to alter the natural hydrology of rivers by making long and severe low water periods more common in some river basins (Costa and Foley 1999). Highly productive river-floodplain ecosystems provide food sources for human communities globally (Bayley 1981, Thilstead et al. 1997, Choo and Williams 2003). However, hydrologic alternations and mismanagement of river-floodplain fisheries threaten fish populations and jeopardize the food security of millions of people (Ziv et al. 2012, Castello et al. 2013).

As hydrologic alterations increase globally, proper management of river-floodplain fisheries necessitates a thorough understanding of flood pulse influences on fish populations and catches. Specific aspects of flood pulses, here called flood pulse variables, that have the strongest influences on catches have not been evaluated, and the interannual lags of flood pulse effects on catches could vary by taxa. Evaluating how different flood pulse variables can influence diverse fish populations and catches in future years can advance knowledge of the relative importance of high and low water influences on river-floodplain fisheries. Furthermore, investigating the variation of flood pulse influences on catches of fishes with different life history strategies can advance knowledge of how related and unrelated floodplain fishes are affected by a changing environment. This knowledge may inform implementation of ecosystem based management in modified systems to incorporate flood pulse influences when determining annual catch quotas.

Here I seek to investigate how flood pulses influence catches of river-floodplain fishes. My research goals were to 1) assess which flood pulse variables had the strongest relationships with catches of river-floodplain fish; 2) estimate the interannual lag of flood pulse effects on catches; 3) investigate how flood pulse influences on catches of fishes with different life history strategies affected multispecies catches overall; and 4) investigate if flood pulse influences on catches of periodic or equilibrium strategists differed.

Studying flood pulse influences on fishes of Amazon Basin allows for a unique look into the effects of natural flow regimes on fish populations that may be applied to restoring river-floodplains globally. The Amazon Basin contains vast floodplains and receives seasonal precipitation that forms unimodal flood pulses with a mean amplitude of 10 m (Irion et al. 1997). The majority of the rivers in the basin are undammed, which presents a rare opportunity to study a system with an unaltered hydrologic regimes. The variety of Amazonian habitats support a diversity of fishes, many of which have yet to be described (Reis et al. 2003). Many of the fishes are commercially harvested, however a few taxa comprise a majority of the catches by weight (Batista et al. 1998, Batista and Petrere 2003). Fishing activity represents a substantial source of income and provides the principal source of animal protein among subsistence fishers (Bayley 1981, Batista et al. 1998); 40-94 kg/year of fish is consumed per capita in the region (Isaac & Almeida 2011). Further understanding how flood pulses influence fish populations and catches is necessary for maintaining the food security, health, and income of Amazonian inhabitants, and can guide management efforts to recreate naturally functioning river-floodplain ecosystems.

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Chapter 2: A systematic evaluation of flood pulse relationships with catches of 22 fish taxa in river-floodplains of the Amazon

Abstract

Seasonally fluctuating water levels, known as flood pulses, influence the population dynamics of river-floodplain fishes and associated catches. Different flood pulse variables (e.g. maximum stage and season duration) in a given year have been correlated to catches of river-floodplain fishes in future years, but no study to date has systematically assessed which flood pulse variables and interannual lags have the greatest influences on catches. This study assessed which flood pulse variables have the strongest relationships with catches of river-floodplain fishes and estimated the respective interannual lags of flood pulse effects on catches. We modeled catches in a given year of 22 river-floodplain fish taxa collected from 15,540 fishing trips in the central Amazon Basin as a function of flood pulse variables one, two, and three years prior (i.e., t_{-1}, t_{-2}, t_{-3}) while accounting for the effects of fishing effort, gear, and river stage. The assessments of variables with the strongest relationships to catches were based on changes in model accuracy and precision following the removal of each individual flood pulse variable, as indicated by delta root mean square error (Δ RMSE). Low water flood pulse variables had the strongest relationships with catches among the 22 taxa. Catches among the 22 taxa specific models had the strongest relationship with flood pulse variables two years prior, followed by flood pulse variables three years and one year prior. Overall, our results generally indicate that increases in the magnitude and duration of high water levels increase exploitable fish biomass in future years, while increases in the magnitude and duration of low water levels decrease exploitable fish biomass in future years.

Introduction

Seasonally fluctuating river water levels, known as flood pulses, have strong influences on the ecology of river-floodplain fish populations (Junk et al. 1989, Tockner et al. 2000). High water levels provide critical food and shelter resources to many river-floodplain fish while low water levels in floodplain lakes lower water quality conditions and intensify biotic interactions (Welcomme and Hagborg 1977, Junk et al. 1989). Previous studies have documented relationships between catches of river-floodplain fishes and various flood pulse variables, such as the duration of high water levels (Halls and Welcomme 2004). However, no study to date has identified the flood pulse variables that have the greatest influence on fish catches.

When river water levels rise, fish migrate from river channels and floodplain lakes into the vegetated habitats of the floodplains, where they feed on fruits, periphyton, and detritus, and find shelter from predators, thus increasing their reproductive outputs and growth rates (Welcomme and Hagborg 1977, Bayley 1988, Gomes and Agostinho 1997). When river water levels decline, fish are confined to remnant water bodies and suffer from increased natural mortality rates through increased water temperatures (Junk et al. 1983, Melack and Fisher 1983), reduced dissolved oxygen concentrations (Junk et al. 1983, Melack and Fisher 1983), and increased predation rates (Neves dos Santos et al. 2008). These seasonal processes alter the efficiency of fishing gears, as gear catchability decreases as fish disperse onto the floodplain, and increases when fish are concentrated in receding water bodies (Merona and Gascuel 1993, de Graaf 2003a). Seasonal flood pulse influences on fish biomass in a given year can affect fish biomass available for harvest in subsequent years (Merona and Gascuel 1993, Karenge and Kolding 1995, Chifamba 2000). For example, if few juvenile fish survive in a year due to extreme low water levels, catches of that cohort may be low in future years, after the time it takes for the cohort to be recruited into the fishery. The seasonal and interannual effects of flood pulses on fish populations are therefore linked and result in highly dynamic fish populations and catches (Lagler et al. 1971, Moses 1987, Merona and Gascuel 1993).

Catches of river-floodplain fish have been correlated to various flood pulse variables, defined here as characteristics of the hydrologic regime (e.g. maximum stage), with associated interannual lags (Holcik and Kmet 1986, Moses 1987, Merona and Gascuel 1993). Multispecies catches in a given year were positively correlated to a high water index (HWI), defined as the area between the stage curve and the level at which floodplains become submerged (i.e. bankfull level), of the previous year in a Nigerian floodplain system (Moses 1987). In that study, it was inferred that higher water levels and longer duration of high water allow fish populations to utilize more of the floodplain resources. Catch per unit effort (CPUE) of multispecies catches in a given year in the Central Amazon was found to be positively correlated to a HWI three years prior and to a low water index (LWI, the area between the stage curve and below bankfull level) two years prior (Merona and Gascuel 1993). In that study, it was inferred that high and low water levels affect rates of recruitment and mortality of juvenile fishes and thus fish biomass available for harvest in future years. Multispecies catches of river-floodplain fish in the Lower Amazon in a given year were positively correlated to high water levels and negatively correlated to low water levels two and three years prior (Castello et al. 2015). In the same region, another study found positive correlations between multispecies catches in a given year and mean water levels two to three years prior (Isaac et al. 2016). Other flood pulse variables that have been correlated to fish population dynamics include amplitude between high and low water levels of previous years (Karenge and Kolding 1995, Chifamba 2000), river discharge (Holcik and Kmet 1986), and the duration of low water levels (Welcome and Hagborg 1977), among others.

Despite this body of understanding of flood pulse influences on fish populations, no systematic analysis to date has considered possible relationships between a broad range of flood pulse variables in a given year and floodplain fish catches in future years. The objectives of our study were to: 1) assess which flood pulse variables have the strongest relationships with catches of river-floodplain fish; and 2) estimate the interannual lag of flood pulse effects on catches. As the natural hydrology of many rivers globally is being increasingly altered, addressing these questions is important for the many efforts to restore the hydrology of highly modified rivers (Rosenberg et al. 2000, Palmer et al. 2005). Improved understanding of the relationships between fish catches and flood pulse characteristics may guide management and restoration of river-floodplain fisheries and hydrological cycles. Our study focused on the central Amazon Basin, where extensive floodplains and an unaltered hydrological regime make it an ideal system to study the relationships between flood pulses and fish catches.

Methods

General Methods

Catches of 22 river-floodplain fish taxa from 15,540 fishing trips were modeled as a function of fishing effort, fishing gear, and flood pulse variables over three time periods (t_{-1}, t_{-2}, t_{-3} years). Total fishing effort for each trip was adjusted to correspond to the percentage that each taxa contributed to total multispecies catch. Three flood pulse variables representing the observed range of flood pulse variability were selected for the analysis after a Principal Components Analysis (PCA) was used to reduce collinearity among an initial set of nine candidate explanatory variables. Candidate models were selected using A Least Absolute Shrinkage and Selection Operator (LASSO, Tibshirani 1996). Once final models for each taxa were selected, each selected flood pulse variable was removed and changes in the square root mean square error (Δ RMSE) of the models were calculated to assess the ability each variable to explain catches. The flood pulse variables and associated time lags with the strongest relationships to catches of river-floodplain fish were assessed based on the sums of Δ RMSE associated with the removal of individual flood pulse variables among the 22 taxa specific models.

Study area

The Amazon Basin (Figure 1.1) drains about 20% of worldwide continental freshwater (Meybeck and Ragu 1996), receiving seasonal precipitation that forms long unimodal flood pulses with a mean amplitude of approximately 10 m (Irion et al. 1997). These flood pulses vary, as they are influenced by interannual variability (e.g., El Niño-Southern Oscillation; Schöngart and Junk 2007). Most of the commercial fishery operations in the study area target fishes as water levels recede and fish migrate from floodplains to river channels. Fishes belonging to five main taxa, *Semaprochilodus spp.*, *Prochilodus spp.*, *Mylossoma spp.*, *Brycon spp.*, and *Triportheus spp.*, comprise approximately 77% of all landings by weight in the city of Manaus, Brazil (Batista and Petrere 2003). Commercial fisheries mainly utilize purse seines and gill nets (Almeida et al. 2003), although other gears such as rods, cast nets, and harpoons are also used (Batista et al. 2000). The majority of fish production landed in Manaus comes from the Purus, Amazon-Solimões, and Madeira rivers, though much of this comes from locations close to Manaus. These fisheries are extremely important; mean annual catch landed in Manaus is approximately 6.26×10^8 kg (Batista and Petrere 2003), and 40-94 kg/year of fish is consumed per capita in the region (Isaac & Almeida 2011).

Data Sources

Fishery Data

Commercial fishing trip data of fish landings in Manaus were collected through fishery surveys between 1994 and 2004, including catch of each taxa (henceforth referred to as taxa specific catch), number of days spent fishing, number of fishers per boat, amount of fuel used, types of gears used, date of arrival, and the river where fishing took place. Only fishing trips from the Amazon-Solimões, Madeira, and Purus rivers using a single gear type (either gillnets or seines) were used in this analysis. The taxa used in this study (Table 1.1) were carefully selected based on the availability of catch data. Only taxa that were caught on at least 50 fishing trips that were evenly distributed among study years were selected, resulting in a total of 15,540 fishing trips from 1994 to 2004 encompassing 22 taxa that account for ~94% of the annual landing.

Measures of total fishing effort for each trip were adjusted for each taxa specific catch, because the total (multispecies) effort of fishing trips did not always reflect the effort expended to catch each taxa. For example, the total effort for a fishing trip would not adequately represent the catch of a taxa that happened to be caught in a net while targeting a different taxa. Taxa specific catches for each fishing trip were sorted into four possible catch composition scenarios (Figure 1.2): 1) ‘single taxa’ when only one taxa was caught, 2) ‘targeted’ when taxa specific catch composed greater than 50% of the total catch, 3) ‘untargeted’ for all other taxa in the trip that did not compose greater than 50% of the total catch, or 4) ’even’ when no taxa specific catch was greater than 50% of the total catch.

Hydrologic data

A review of studies investigating the relationship between catches of river-floodplain fish and flood pulses led to the calculation of nine flood pulse variables (Table 1.2) based on available river height data (stage) measured by the Agência Nacional de Águas at the Manacapuru station (ANA, 2016). Nine flood pulse variables were calculated for each year between 1991 and 2004 to encompass the data range of catches with time lags of t_{-1}, t_{-2}, and t_{-3}. The study period encompassed years with extreme hydrological events (i.e. 1995, 1997, 1999) as well as normal hydrology (e.g. 1996, 2000, 2001; Figure 1.3). Maximum stage (MaxS, cm) was defined as the highest water height observed during each year, while minimum stage (MinS, cm) was defined as the lowest water height. Mean stage (MeanS, cm) was calculated as the average water level of each year. Relative bankfull level, the level at which water spills out of main channels and floodplains become inundated, was estimated based on the method used by Castello et al. (2015). The duration of high and low water levels were calculated as the number of days that stage was above relative bankfull level for high water (HWD), and below relative bankfull level for low water (LWD). HWI_1, LWI_1, HWI_2, and LWI_2 indices (Figure 1.4) were calculated using integration, as follows. HWI_1 was calculated as the area between the stage curve and above relative bankfull level, while LWI_1 index was calculated as the area between the stage curve and below relative bankfull level. HWI_2 index was calculated as the area between the stage curve and relative bankfull level from the time of relative bankfull level to the time of maximum stage, while LWI_2 index was calculated as the area between the stage curve and relative bankfull level from the time of relative bankfull level to the time of minimum stage. These high and low water indices were developed to estimate both the duration and severity of high and low water periods (Kapetsky et al. 1974).

A PCA using a correlation matrix (9 x 9) generated from the above-derived flood pulse variables was conducted to ordinate flood pulse variable measurements (Figure 1.5). Three principal component axes explained 97% of the variation among flood pulse variables (Figure

A.1), and the flood pulse variable with the highest loading for each principal component axis was chosen to maximize orthogonality among axes. Three variables, MaxS, HWD, and LWI_2, were selected to represent variation of the annual flood pulse of the central Amazon basin.

Data Analysis

Taxa specific catches per trip for each of the 22 taxa were modeled using generalized linear models as a function of the following full set of candidate explanatory variables: adjusted fishing effort (categorical), gear (categorical), stage at the time of landing (two variables, continuous and categorical), and flood pulse variables of previous years. Available information for some of the taxa in the study area indicate that they are recruited to the fishery between 1.5 and three years after hatching (e.g. 19 months for *P. nigricans*; 33 months for *Pseudoplatystoma fasciatum*; Barthem and Fabre 2004, Isaac et al. 2016). To account for flood pulse influences on recruitment of the studied taxa, flood pulse variables one, two, and three years before the year fishing took place (t_{-1}, t_{-2}, and t_{-3} respectively, Table 1.2) were considered in models. Stage at the time of landing of the river where fishing took place was used to account for water level influences on gear catchability. A categorical variable indicating whether stage was rising or falling was used to further delineate the seasonal influence of the flood pulse on catches, as gear catchability is often different for rising and falling waters at the same stage. The full model used for each taxa was:

$$C_i = \beta_0 + \beta_1 S + \beta_2 R + \beta_3 nD + \beta_4 nF + \beta_5 D + \beta_6 Tg + \beta_7 U + \beta_8 Ev + \beta_9 Gn + \beta_{10} FPV_1 + \beta_{11} FPV_2 + \ldots \beta_{18} FPV_9 + \epsilon_i$$

where C_i is the $\log_{10}$ transformed catch per trip at time t (kg; catch per taxa per trip was log transformed to satisfy the assumption of normality), S is stage at time of landing (cm), R is a categorical variable to denote if water levels were rising or falling (1 for rising, 0 for falling), nD is the number of days spent fishing, nF is the number of fishers per trip, D is the amount of diesel used per trip, Tg is a categorical variable for the 'targeted' catch category, U is a categorical variable for the 'untargeted' catch category, Ev is a categorical variable for the 'even' catch category, Gn is a categorical variable for gear (0 for seine net, 1 for gillnet), FPVs are flood pulse variables at t_{-i} years (see Table 1.2), $\beta_0 - \beta_{18}$ are fitted parameters, and ε_i is error. All flood pulse variables were scaled by their standard deviations and centered by their variable means, so that later in the analysis process they could be systematically analyzed for their relationships to catches. All regressions were conducted using the "glmnet" package (version 2.0-2) with a Gaussian link function in R (version 3.1.2).

A Least Absolute Shrinkage and Selection Operator (LASSO, Tibshirani 1996) was used as a model selection criteria because it is fairly tolerant to collinearity present among candidate effort variables (Dormann et al. 2013). The LASSO penalized regression procedure fits generalized linear models in an iterative fashion by simultaneously investigating each variable's ability to explain the response variable and adjusting parameter values using a scaling factor λ. LASSO is different from ridge regression in that it adjusts parameter values to zero if variables have little ability to explain the response variable. The LASSO procedure will only stop once the maximum amount of variance that can be explained by the data has been explained, often resulting in the selection of many variables that have little explanatory power. To avoid the inclusion of flood pulse variables that have little ability to explain taxa specific catches, the RMSE was calculated for each LASSO step and values of the scaling factor λ were chosen once the rate of RMSE decrease with each step drastically declined (usually between step 20 and 40).

Following model fitting, plots of the residuals were checked to assess if the models satisfied assumptions of linearity, normality, and homoscedasticity.

The flood pulse variables and interannual lags that had the strongest relationships with catches of river-floodplain fishes were evaluated based on the ability of each flood pulse variable to reduce error in predicting catches. After final models had been selected and model RMSE had been calculated, each flood pulse variable was individually removed to calculate Δ RMSE, the difference in RMSE between each taxa specific (full) final model and the same model without the flood pulse variable of interest. This procedure was done for every selected flood pulse variable in all 22 taxa specific models. The sums of Δ RMSE for each flood pulse variable across all 22 models was calculated in two ways: 1) by variable type (e.g. MaxS) to assess which flood pulse variable had the strongest relationships with catches of river-floodplain fish, and 2) by interannual lag (e.g. t_{-1}) to assess which lag had the strongest relationships with catches. To assess whether relationships between flood pulse variables and fish catches were positive or negative, the standardized parameter estimates of the flood pulse variables selected in the 22 models were also calculated. The sums of the standardized parameter estimates as well as their respective absolute values for all 22 models were grouped using the same methods used for Δ RMSE.

Results

Model fits

The models generally explained catches of river-floodplain fish well, mean RMSE and R^2 among models were 0.31 and 0.50, respectively (Figure 1.6). The accuracy of models were comparable to studies using fishery independent data (Goñi et al. 1999, Wingle et al. 2010). Mean partial R^2 among models for effort, stage at the time of catch, gear, and flood pulse variables were 0.37 ± 0.12, 0.01 ± 0.02, 0.04 ± 0.04, and 0.08 ± 0.07, respectively. All 22 models satisfied the assumptions of normality, linearity, and homoscedasticity (Figure A.2). The effort adjustment procedure simultaneously reduced RMSE and increased R^2 values by an average of 16.5% and 265.5%, respectively (Figure 1.7).

Relationships between flood pulse variables and catches

LWI_2 was the flood pulse variable that had the strongest overall relationship with catches across all 22 taxa specific models (Δ RMSE = 1.36), followed by MaxS (Δ RMSE = 1.24) and HWD (Δ RMSE = 0.70, Table 1.3). MaxS and HWD mostly had positive relationships with catches (Figure 1.8). LWI_2 mostly had negative relationships with catches (Figure 1.8) and was the only flood pulse variable that was selected by all models at least once. LWI_2 at t_{-2} was the flood pulse variable with a specific lag that had the strongest relationship with taxa specific catches (Δ RMSE = 0.52, Table 1.4), followed by MaxS at t_{-2} (Δ RMSE = 0.49) and MaxS at t_{-3} (Δ RMSE = 0.48). LWI_2 at t_{-3} had the strongest negative relationship with catches (sum of standardized parameter estimates = -1.02) while MaxS at t_{-3} years had the strongest positive relationship (sum of standardized parameter estimates = 0.90).

Flood pulse variables with a lag of t_{-2} had the strongest relationship with catches across all 22 taxa specific models (Δ RMSE = 1.33) compared to flood pulse variables with a lag of t_{-3} (Δ RMSE = 1.26) and t_{-1} (Δ RMSE = 0.71, Table 1.5). Sums of the standardized parameter estimates of flood pulse variables at t_{-1}, t_{-2}, and t_{-3} indicated mixed positive and negative relationships with catches. However, flood pulse variables at t_{-1} mostly had positive relationships with catches while flood pulse variables at t_{-2} and t_{-3} mostly had negative relationships with catches (Table 1.4, Figure 1.8). For example, catches of *Mylossoma spp.* and

Oxydoras niger had stronger positive relationships to MaxS at t_{-1} compared to weaker negative relationships between catches of *S. insignis* and *C. macroponum* and LWI_2 at t_{-1}.

Discussion

Influences of flood pulse variables on catches

The results of this study are consistent with the prevailing view that high water levels increase fish biomass available for harvesting, as MaxS and HWD mostly had positive relationships with catches, while low water levels decrease fish biomass, as LWI_2 mostly had negative relationships with catches (Figure 1.8; Junk et al. 1989, Bayley 1991, Halls and Welcomme 2004). In line with a previous study (Castello et al. 2015), Δ RMSE of LWI_2 (= 1.36) was only slightly greater than Δ RMSE of MaxS (= 1.24; Table 1.3), indicating that high water levels may be as influential to catches as low water levels. The strong flood pulse influences with two and three year lags on catches of river-floodplain fish are also consistent with previous studies that used different datasets and found similar lags in fisheries of the Amazon Basin (Merona and Gascuel 1993, Castello et al. 2015, Isaac et al. 2016). However, catches of some taxa had negative relationships with high water levels and positive relationships with low water levels, contrary to prevailing views that high waters always enhance fish production and low water levels always reduce fish biomass. Overall, these systematic results indicate that both high and low water levels in a given year control fish catches for a majority of the studied taxa two and three years later.

Flood pulse variables measuring characteristics of high water levels generally had positive relationships with catches in subsequent years likely because increased access to floodplains tends to increase fish reproductive outputs and body growth rates (Lagler et al. 1971, Kapetsky 1974). MaxS, and other positively correlated high water flood pulse variables including HWI_1, HWI_2, and MeanS, likely had positive relationships with catches because they correspond to the flooded area of the floodplain that can provide food and shelter for fish populations. A larger flooded floodplain area can provide fish with access to greater amounts of periphyton, fruits, detritus, and macroinvertebrates that could be utilized as food (Welcomme 1985, Merona and Rankin-de-Merona 2004, Halls and Welcomme 2004). Furthermore, greater flooded areas could also disperse fish over larger areas, leading to reduced predation rates and thus reduced natural mortality rates. In any given year, increased growth rates due to greater access to floodplain habitats and food availability (Lagler et al. 1971), combined with reduced natural mortality rates, could lead to increased biomass available for harvest in subsequent years. HWD likely had a similar relationship with catches as MaxS and other high water flood pulse variables because access to floodplain resources for a longer period of time would be beneficial for fish reproduction, body growth, and survival (Halls and Welcomme 2004). However, it has been suggested that if high water levels persist for too long, stagnant water may lead to an excess of decomposition and hypoxia that could be detrimental to river-floodplain fish populations (Junk et al. 1989, Bayley 1991). This phenomenon may explain the consistent negative relationships found between catches and HWD among all time lags for the taxa *S. taeniurus* and *Osteoglossum bicirrhosum*.

Flood pulse variables measuring characteristics of low water levels generally had negative relationships with catches likely because long and severe low water levels increase fish mortality rates in floodplain lakes (Magoulik and Kobza 2003, Halls and Welcomme 2004). LWI_2, and other highly correlated flood pulse variables including LWI_1, LWD, and MinS, are speculated to be the flood pulse variables that account for the period of the flood pulse associated with the greatest fish mortality rates. Low water levels limit available habitat for fish populations to floodplain lakes and river channels that frequently undergo hypoxia, which few fish can tolerate (Magoulik and Kobza 2003, Fontenot et al. 2011). Confined fish are often subjected to higher rates of predation due to higher concentrations of predators (Holcik and Kmet 1986, Schlosser et al. 2000) and the negative influence of hypoxia on their ability to escape predators (Domenici et al. 2007). Water temperatures could also increase during low water levels and could exacerbate mortality rates induced by hypoxia (Tramer 1977).

Interannual lag of flood pulse effects on catches

The two and three year lags of flood pulse effects on catches of river-floodplain fish were roughly similar to the age of the fishes at the time they were caught (1.5 – 3 years of age; Isaac et al., 2016), suggesting that flood pulses have the greatest influence on fish populations during larval and juvenile life stages. Conditions that are favorable for the survival and growth of larval fish can be expected to increase recruitment to the fishery in future years, while conditions that increase mortality rates can be expected to decrease recruitment. For example, the positive influences of MaxS on *S. insignis* (Figure 1.8) could have increased the reproductive success of young of the year cohorts and increase catch in future years once the cohort has been recruited to the fishery (de Graaf 2003, Halls and Welcomme 2004). Two and three year lags between water level indices and catches of floodplain fishes were found in the central and lower Amazon regions (Merona and Gascuel 1993; Castello et al. 2015), but those studies did not provide estimates of the age at recruitment for targeted fishes. Isaac et al. (2016) divided fish taxa in the lower Amazon region into three longevity groups and found that their mean ages at catch, between 21, 27, and 34 months, were roughly similar to the lags of the flood pulse variables with which they were correlated to.

The influence of flood pulse variables at t_{-1} was weaker than that for t_{-2} and t_{-3}, but it was important. Flood pulse variables at t_{-1} could affect individuals of fish populations during their adult and sub-adult life stages by influencing natural mortality rates of adult or sub-adult fish in t_{-1} years (Freitas et al. 2013) or by influencing growth rates in t_{-1} years (Lagler et al. 1971, de Graaf 2003).

Variations among taxa

Our results indicate that flood pulse influences on taxa do not always conform to general expectations that high water levels increase, and low water levels decrease, catches. For example, MaxS at t_{-3} and t_{-2} had negative relationships with catches of *Hypopthalmus spp.*. Such differences in fish responses to flood pulses could be due to differences in life history traits among the studied taxa. For example, high and low water levels can influence the availability of food sources in different ways for fish possessing different feeding strategies (Santos et al. 2008) and consequently influence their body condition (Abujanra et al. 2009). Castello et al. (2015) found that the magnitude of both high and low water level influences on catches were greater for herbivores than piscivores and omnivores. Further research is necessary to understand how catches of fishes with different life history traits are influenced by the flood pulse.

Implications

The results of this study demonstrate the need to consider the influences of flood pulses on fish populations when managing river-floodplain fisheries. While predictive models were not created in this study, the identification of flood pulse variables and lags important to Amazonian fisheries further informs the creation of models that can predict the relationships between flood pulses in a given year and catches in future years. The maximum stage, high water duration, and low water index should be considered when predicting catches of future years in river-floodplains. However, the high degree of collinearity present among the ten candidate flood pulse variables indicates that the specific flood pulse variables used to manage fisheries can vary as long as the variables accurately describe the dynamics of the flood pulse in the region of interest. Proper management should incorporate measures of both high and low water levels of previous years when determining catch regulations in a given year. In the Amazon, multispecies catch limits for any given year two and three years after severe low water levels must be conservative because for most taxa, severe low water levels decrease catches in future years. The results of this study can also be used to improve taxa specific management of Amazonian river-floodplain populations by providing taxa specific information of how various measures of high and low water levels in a given year influence catches in future years. As the escalation of hydrologic alterations continues to affect flood pulses in the Amazon basin, increasing magnitude and frequency of extreme low water levels (Macedo and Castello 2016), the results of this study provide additional information on the characteristics of the flood pulse that need to be restored in order to maintain the fish catches that sustain the income and food security services that floodplain communities depend on.

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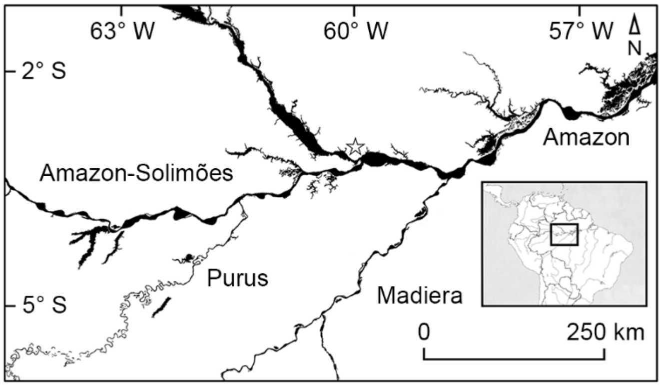

Figure 1.1. The study area in the central Amazon Basin. Fishing trips used in this study were conducted in close proximity to Manaus, Brazil (location marked by star), on the Madeira, Purus, and Amazonas rivers.

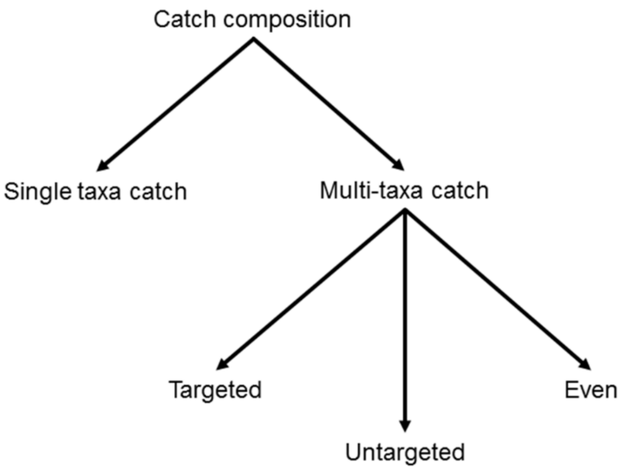

Figure 1.2. Decision tree used to adjust taxa specific fishing effort by categorizing it based on catch composition of each fishing trip.

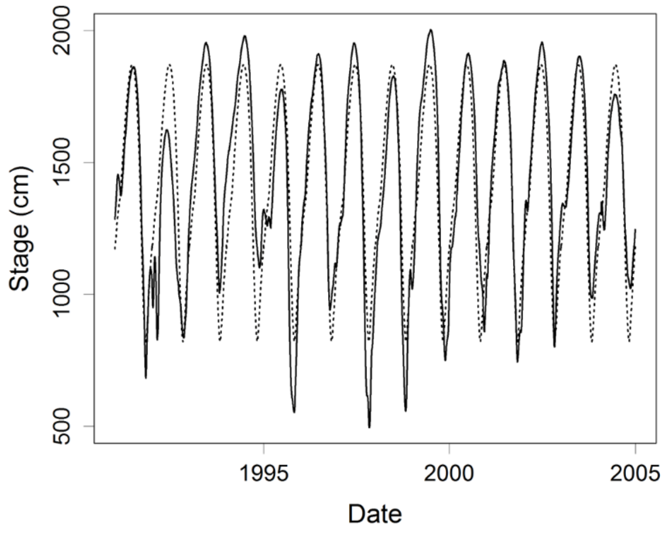

Figure 1.3. Daily stage measured by the Agência Nacional de Águas at the Manacapuru station from 1991 through 2004. The solid line represents daily stage measurements while the dotted line represents daily mean stage measurements during the study period.

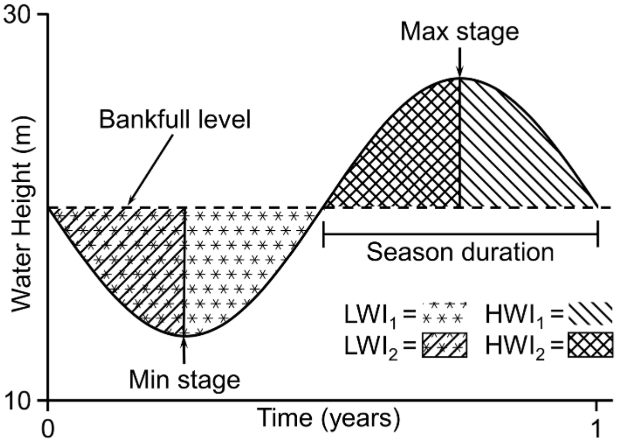

Figure 1.4. Schematic diagram of a unimodal flood pulse cycle, showing some flood pulse variables used in this study.

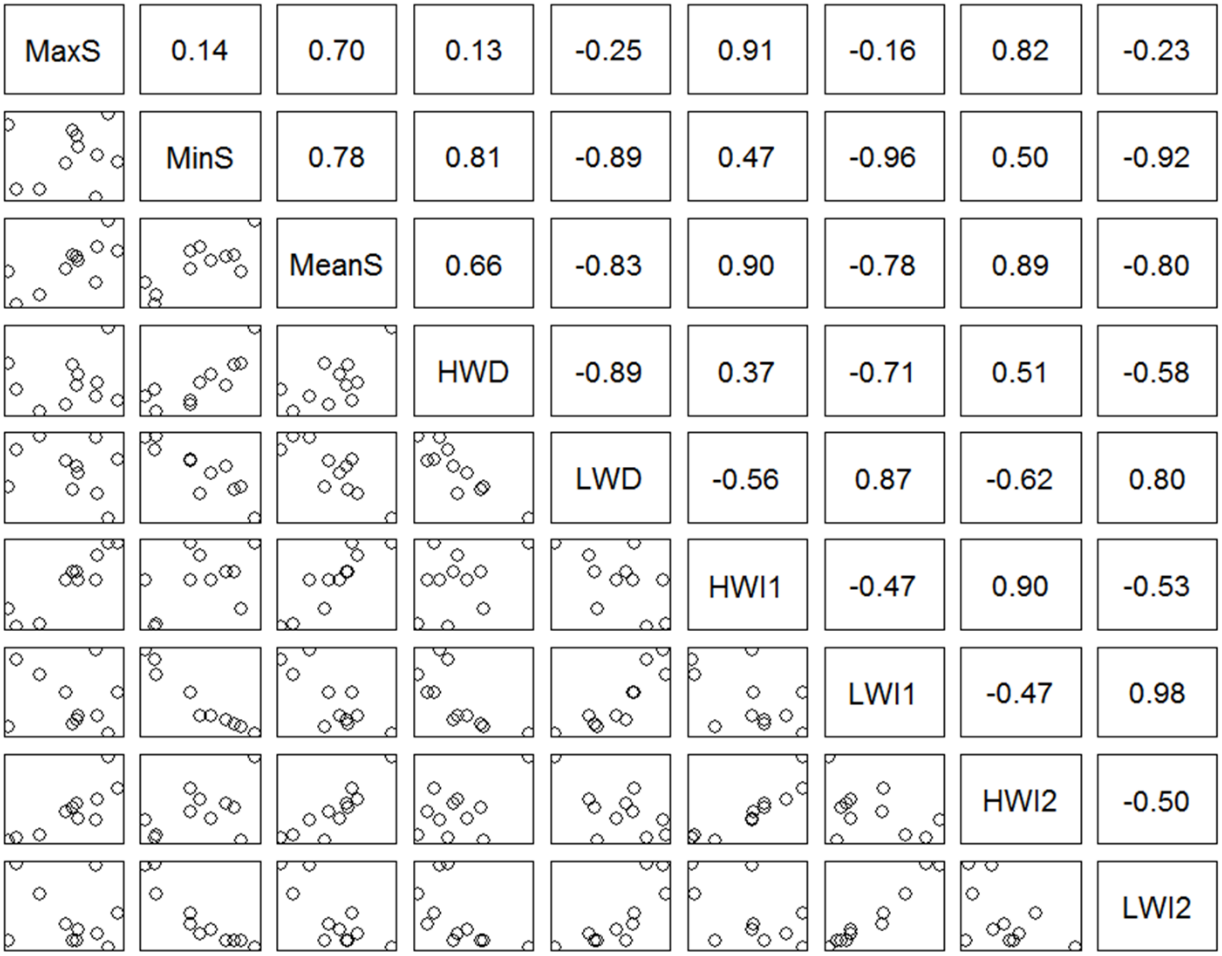

Figure 1.5. Scatterplot and correlation matrix of all initial candidate flood pulse variables.

Values above the diagonal represent the correlation between pairs of variables.

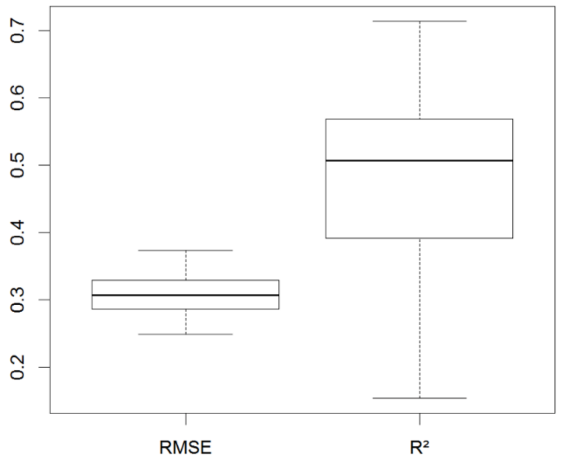

Figure 1.6. Boxplots of root mean square error (RMSE) and variance explained (R^2) among models for all 22 taxa.

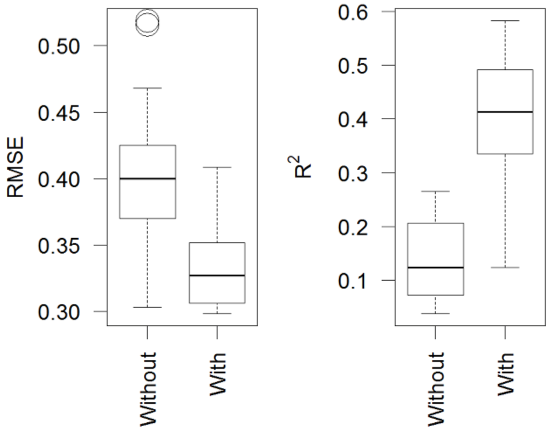

Figure 1.7. Root mean square error (RMSE) and R^2 with and without effort adjustment procedure used to adjust total multispecies fishing effort to taxa specific effort.

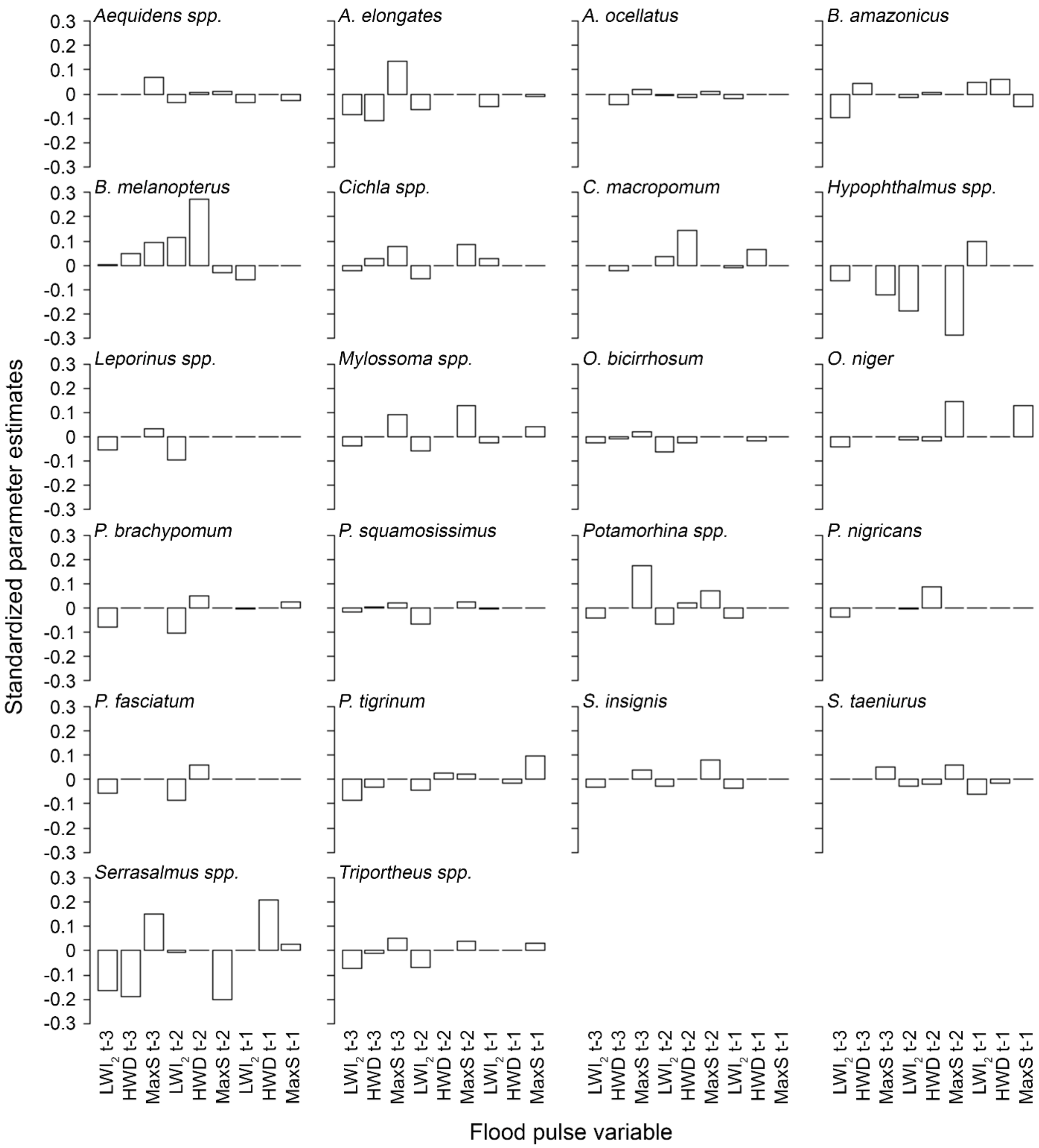

Figure 1.8. Standardized parameter estimates of flood pulse variables for all 22 taxa. Positive values indicate positive relationships with catches, while negative values indicate negative relationships with catches.

Table 1.1. Commercially important fishes of the central Amazon Basin modeled in this study. Scientific names for each taxa were collected from fishbase.org. Life history strategy classifications of studied taxa as defined by Röpke et al (in review) denoted by Xs. Taxa identified as Piranha were not analyzed in Chapter 2.

Species	Common Name	Order	Family	Periodic	Equilibrium
Uaru amphiacanthoides *Acarichthys heckelli* *Acaronia nassa* *Aequidens spp.* *Caquetaia spectabilis* *Chaetobranchus flavescens* *Chaetobranchus orbicularis* *Cichlassoma amazonarum* *Geophagus proximus* *Geophagus spp.* *Heros spp.* *Satanoperca acuticeps* *Satanoperca jurupar* *Symphysodon aequidens*	Acará	Perciformes	Cichlidae		X
Astronotus ocellatus *Astronotus crassipinis*	Acará-açu	Perciformes	Cichlidae		X
Schizodon fasciatus *Leporinus friderci* *Leporinus tigrinus* *Leporinus affinis* *Anostomoides laticeps*	Aracu	Characiformes	Anostomidae	X	
Osteoglossum bicirrhosum	Aruanã	Osteoglossiformes	Osteoglossidae		X
Potamorhina altamazonica *Potamorhina latior* *Potamorhina pristigaster* *Psectrogaster amazonica* *Caenotropus labyrinthicus*	Branquinha	Characiformes	Curimatidae, Chilodontidae	X	
Pseudoplatystoma tigrinum	Caparari	Siluriformes	Pimelodidae	X	
Anodus elongates *Hemiodus microlepis* *Hemiodus unimaculatus*	Cubiu	Characiformes	Hemiodontidae	X	
Oxydoras niger	Cuiú-cuiú	Siluriformes	Doradidae	X	

Table 1.1. (Continued)

Species	Common Name	Order	Family	Periodic	Equilibrium
Prochilodus nigricans	Curimatã	Characiformes	Prochilodontidae	X	
Semaprochilodus taeniurus	Jaraqui-fina	Characiformes	Prochilodontidae	X	
Semaprochilodus insignis	Jaraqui-grossa	Characiformes	Prochilodontidae	X	
Brycon melanopterus	Jatuarana	Characiformes	Characidae	X	
Hypopthalmus edentates *Hypopthalmus marginatus*	Mapará	Siluriformes	Pimelodidae	X	
Brycon amazonicus	Matrinxã	Characiformes	Characidae	X	
Mylossoma aureum *Mylossoma duriventris* *Myleus schomburgkii* *Metynnis argenteus* *Metynnis hypsauchen* *Myloplus torquatus*	Pacu	Characiformes	Serrasalmidae	X	
Plagioscion squamosissimus	Pescada	Perciformes	Sciaenidae	X	
Piaractus brachypomum	Pirapitinga	Characformes	Serrasalmidae	X	
Pygocentrus natterei *Serrasalmus rhombeus* *Catoprion mento*	Piranha	Characiformes	Serrasalmidae	N/A	N/A
Triportheus albus *Triportheus angulatus* *Triportheus auritus* *Triportheus elongates* *Triportheus trifurcatus*	Sardinha	Characiformes	Triporthidae	X	
Pseudoplatystoma fasciatum	Surubim	Siluriformes	Pimelodidae	X	
Colossoma macropomum	Tambaqui	Characiformes	Serrasalmidae	X	
Cichla monoculus *Cichla ocellaris*	Tucunare	Perciformes	Cichlidae		X

Table 1.2. Flood pulse variables considered as candidate explanatory variables to describe natural flood pulses of the Amazon Basin.

Hydrological variable	**Abbreviation**
Mean annual stage	(MeanS)
Maximum stage	(MaxS)
Minimum stage	(MinS)
High water duration	(HWD)
Low water duration	(LWD)
HW index 1	(HWI_1)
LW index 1	(LWI_1)
HW index 2	(HWI_2)
LW index 2	(LWI_2)

Table 1.3. Sums of delta root mean square error (Δ RMSE), absolute parameter estimates, and parameter estimates of flood pulse variable types among models for 22 taxa. For abbreviation definitions, see Table 1.2.

Flood pulse variables	**Δ RMSE**	**Absolute parameter value**	**Parameter value**
LWI_2	1.357	2.769	-2.124
MaxS	1.242	2.778	1.327
HWD	0.701	1.661	0.596

Table 1.4. Sums of delta root mean square error (Δ RMSE), absolute parameter estimates, and parameter estimates of flood pulse variables among models for 22 taxa. Abbreviation definitions can be found on Table 1.2 while -i indicates the lag period for the variable (e.g. MaxS $_{t-1}$ = maximum stage of one year prior to year t_0).

Variable	**Δ RMSE**	**Absolute parameter value**	**Parameter value**
LWI2-2	0.522	1.248	-0.944
Max S-2	0.493	1.191	0.159
Max S-3	0.483	1.149	0.903
LWI2-3	0.451	1.015	-1.015
HWD-2	0.317	0.744	0.593
HWD-3	0.327	0.538	-0.285
LWI2-1	0.384	0.507	-0.166
Max S-1	0.266	0.439	0.265
HWD-1	0.057	0.379	0.287

Table 1.5. Sums of delta root mean square error (Δ RMSE), absolute parameter estimates, and parameter estimates of flood pulse variables of t_{-1}, t_{-2}, and t_{-3} years among models for 22 taxa.

Time lag	**Δ RMSE**	**Absolute parameter value**	**Parameter value**
t_{-2}	1.332	3.182	-0.192
t_{-3}	1.261	2.702	-0.396
t_{-1}	0.707	1.324	0.386

Appendix A

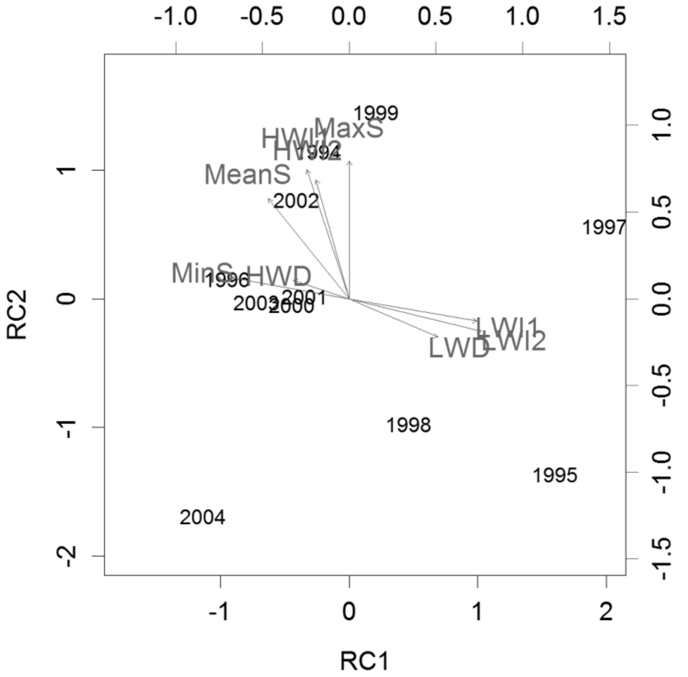

Figure A.1. Biplot ordination of candidate flood pulse variables used to select flood pulse variables to use in taxa specific models.

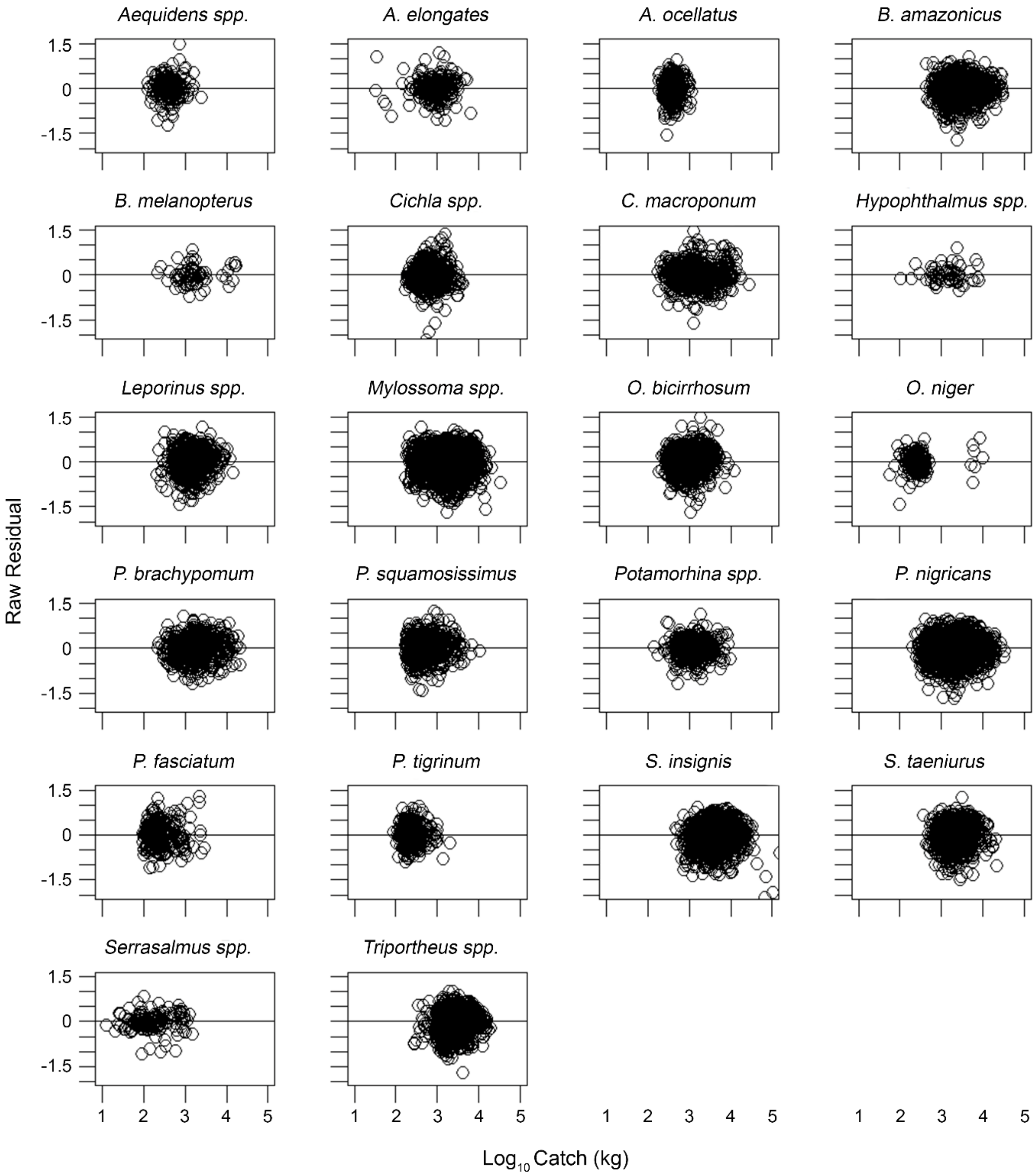

Figure A.2. Raw residual plots for 22 taxa modeled in study.

Table A.1. Flood pulse variable calculations for each year used in the study.

Year	MaxS	MinS	MeanS	HWD	LWD	HWI_1	LWI_1	HWI_2	LWI_2
1991	1862	683	1434.115	301	158	134915	23640	30248	6127
1992	1623	828	1207.341	169	112	58625	17430	27451	10654
1993	1955	1005	1556.679	299	34	155403	1079	92391	750
1994	1979	1101	1618.926	365	15	159993	111	120067	63
1995	1777	552	1274.492	277	106	99242	36857	61981.5	22845.5
1996	1911	941	1475.613	282	85	138797	6742	86694	2024
1997	1952	495	1362.654	267	122	132435	41592	74653.5	22668
1998	1828	557	1312.404	244	125	101122	29049	64376	14651
1999	2003	749	1493.86	261	94	159997	20744	97932	9363.5
2000	1914	858	1454.484	298	76	132596	8664	75589.5	4816.5
2001	1886	744	1421.239	254	92	132812	20243	81112	6338.5
2002	1956	801	1512.36	287	49	151061	8522	89530.5	3676
2003	1902	986	1480.438	312	54	138987	4710	83980.5	2073
2004	1758	1022	1409.234	315	57	112230	3281	60275	2001

Chapter 3: Flood pulse influences on catches of Amazonian fishes in relation to life history strategies

Abstract

Seasonally fluctuating water levels, known as flood pulses, influence the population dynamics of river-floodplain fishes and associated catches. Although flood pulse influences on fish populations are expected to vary among fishes with different biological traits, previous studies have not systematically compared the influences on catches of fishes with different life history strategies. This study sought to assess how flood pulses may have different influences on catches of fishes with different life history strategies. We modeled catches in a given year of 21 river-floodplain fish taxa collected from 18,834 fishing trips in the central Amazon Basin as a function of flood pulse variables of prior years to investigate the different influences that flood pulses can have on catches of different taxa. Flood pulse influences on multispecies catches overall and on taxa with different life history strategies were assessed by comparing parameter estimates associated with flood pulse variables among models. Flood pulse influences on multispecies catches overall appeared to be most influenced by relationships between flood pulses and catches of periodic strategists. Flood pulses had greater influences on catches of taxa identified as periodic strategists compared to catches of taxa identified as equilibrium strategists. However, variation was observed in the relationships between flood pulse variables and catches of taxa with the same life history, suggesting that taxa with the same life history strategies do not always respond to flood pulses in the same way. While our findings generally support predictions of how reproductive traits can influence responses to environmental resource fluctuations, other biological traits of individual taxa may further explain responses to flood pulse influences.

Introduction

Seasonal water level fluctuations in river-floodplain ecosystems, known as flood pulses, (Junk et al. 1989), influence fish population dynamics (Lagler et al. 1971, Halls and Welcomme 2001, de Graaf 2003), fishery dynamics (Welcome and Hagborg 1977), and fish catches (Merona and Gascuel 1993, de Graaf 2003). Previous studies have shown that high water levels enable fishes to use floodplain food and shelter resources that foster body growth and reproduction processes, while low water levels confine fishes in remnant water bodies where they are more susceptible to higher rates of natural and fishing mortality (Welcomme and Hagborg 1977). However, it is unclear how flood pulse influences on catches can vary among fishes possessing different life history traits.

Flood pulses can have strong influences on fish population dynamics. As fish move from river channels and lakes to vegetated floodplain habitats during high water levels, their growth and survival rates tend to increase due to abundant food resources and submerged vegetation that provide shelter from predators (Welcomme and Hagborg 1977, Bayley 1988). Low water levels confine fish to river channels or lakes where increased water temperatures, reduced dissolved oxygen concentrations, and increased predation rates tend to increase natural mortality rates (Junk et al. 1983, Melack and Fisher 1983, Neves dos Santos et al. 2008).

Seasonal flood pulse influences also alter the efficiency of fishing gears and can affect fish biomass available for harvest in subsequent years (Merona and Gascuel 1993, Karenge and Kolding 1995, Chifamba 2000). Gear catchability decreases as fish disperse onto the floodplain during high water levels, and increases when fish are concentrated in receding water bodies during low water levels (Merona and Gascuel 1993, de Graaf 2003). High water levels generally increase exploitable biomass in future years by increasing fish growth and fishery recruitment, while low waters generally decrease exploitable biomass in future years by increasing fishing and natural mortality (Lagler et al. 1971, Moses 1987, Merona and Gascuel 1993). In the Amazon Basin, flood pulses in a given year usually influence catches after a lag of two to three years due to the time it takes for juvenile cohorts to be recruited to the fishery (Castello et al. 2015, Isaac et al. 2016, Olsen Chapter 1). The seasonal and interannual effects of flood pulses on fish populations are therefore linked and result in highly dynamic fish populations and catches (Lagler et al. 1971, Moses 1987, Merona and Gascuel 1993).

Flood pulse influences on fish populations are expected to vary among fishes with different biological traits (King et al. 2003, Zeug and Winemiller 2007, Gorski et al. 2011). Fishes have evolved varying oocyte sizes, fecundities, and ages at maturity to maximize reproductive success (Ruffino and Isaac 1995, Godinho et al. 2010). Patterns of reproductive and other biological traits that often covary were used to classify three generalized life history strategies (Winemiller 1989, Winemiller and Rose 1992): 1) fishes with ‘periodic’ life history strategies usually minimize energy investment in each individual offspring, produce greater amounts of smaller oocytes, and have delayed sexual maturity; 2) fishes with ‘equilibrium’ life history strategies usually have greater energy investment in each individual offspring by producing fewer and larger oocytes that are sometimes guarded by adults; and 3) fishes with ‘opportunistic’ life history strategies reach sexual maturity quickly, have shorter life spans, minimize energy investment in each individual offspring, and produce greater amounts of smaller oocytes. These three endpoint strategies represent a trilateral continua of evolutionary tactics that may influence how fishes respond to flood pulses (Winemiller 2005, Zeug and Winemiller 2007).

Previous studies have found evidence of different flood pulse influences on fishes with different life history strategies. In the Amazon Basin, the strengths and directions of flood pulse influences on catches have been shown to vary among taxa possessing different feeding traits and longevities (Castello et al. 2015, Isaac et al. 2016). High water levels in a temperate system had larger effects on the abundance of young-of-year fishes with periodic and opportunistic strategies, compared to fishes with equilibrium strategies (Gorski et al. 2011). Severe low water levels in a tropical system caused regime shifts among river-floodplain fish assemblages, decreasing abundance of periodic, equilibrium, and intermediate strategists (Röpke et al in review). Population dynamics models of exploited river-floodplain fishes have shown how flood pulses affect fishery recruitment for species that may be opportunistic strategists (e.g. *Puntius sophore*, Halls and Welcomme 2004, de Graaf 2003; *Oreochromis spp*. and *Tiliapia spp*., Linhoss et al. 2012).

However, previous studies have not systematically compared the influences of flood pulses on catches of fishes with different life history strategies. According to life history theory, the fitness of periodic strategists relies on their ability to maximize reproductive success in years with favorable environmental conditions, and endure years with poor environmental conditions. The fitness of equilibrium strategists relies on maximizing the survival of each offspring by investing more energy into each oocyte and often guarding their progeny. Therefore, high water levels with favorable floodplain conditions are expected to allow periodic strategists to have greater reproductive success compared to the more consistent reproductive success of fishes with equilibrium strategies (as documented by Gorski et al. 2011). Conversely, low water levels can be expected to influence fishes with different life histories equally, as poor water quality and increased predator density could affect both periodic and equilibrium strategists (as documented by Röpke et al in review). Since periodic strategists tend to capitalize on favorable environmental conditions, becoming highly abundant, flood pulse influences can be expected to cause periodic strategists to dominate commercially important fisheries.

Understanding how interannual resource shifts caused by flood pulses influence multispecies catches is necessary to incorporate ecosystem based fishery management. Fishery management in river-floodplains generally ignores flood pulse influences on fish populations, which increases the risk of overexploitation following periods of high natural and fishing mortality (Castello et al. 2013). Incorporating knowledge of varying flood pulse influences on different fish populations in management decisions could allow for more sustainable fisheries.

Here, we sought to answer the following overarching research question: how do flood pulses influence catches of fishes with different life history strategies? Our specific objectives were to 1) investigate how flood pulse influences on catches of fishes with different life history strategies affect multispecies catches overall, and 2) investigate if flood pulse influences on catches of periodic or equilibrium strategists differ. Flood pulse influences on multispecies catches overall are expected to be dominated by the influences of flood pulses on catches of periodic strategists given that these taxa should be more influenced by flood pulses than equilibrium strategists. Catches of fishes with periodic life history strategies are expected to be affected by flood pulses more than fishes with equilibrium life history strategies, as flood pulses are expected to have a greater influences on the reproductive success and thus fishery recruitment of fishes with periodic life history strategies (Winemiller 2005). With a highly diverse multispecies fishery and unaltered flow regime, the central Amazon Basin is an ideal system to study the influences of the flood pulse on fish assemblage dynamics and multispecies catches.

Methods

Study area

The Amazon Basin (Figure 1.1) drains about 20% of worldwide continental freshwater (Meybeck and Ragu 1996), receiving seasonal precipitation that forms long unimodal flood pulses with a mean amplitude of approximately 10 m (Irion et al. 1997). These flood pulses vary, as they are influenced by interannual climactic variability (e.g., El Niño-Southern Oscillation; Schöngart and Junk 2007). Fishes belonging to five main taxa comprise 75% of all landings by weight in the city of Manaus, Brazil (Table 1.1, Batista and Petrere 2003). Commercial fisheries mainly utilize lampara seines and gill nets (Almeida et al. 2003), although other gears such as rods, cast nets, and harpoons are also used (Batista et al. 2000). The majority of fish production landed in Manaus comes from the Purus, Amazon-Solimões, and Madeira rivers, though much of this comes from locations close to Manaus. These fisheries are extremely important; mean annual catch landed in Manaus is ~280,000 tons (Batista and Petrere 2003), and 40-94 kg/year of fish is consumed per capita in the region (Isaac & Almeida 2011).

Data Sources

Fishery Data

Commercial fishing trip data of fish landings in Manaus were collected between 1994 and 2004, including catch of each taxa (henceforth referred to as taxa specific catch), number of days spent fishing, number of fishers per boat, amount of fuel used, types of gears used, date of arrival, and the river where fishing took place. Only fishing trips from the Amazon-Solimões, Madeira, and Purus rivers were used in this analysis. The taxa used in this study (Table 1.1) were carefully selected based on the availability of catch data. Only taxa that were caught on at least 50 fishing trips that were evenly distributed among study years were selected, resulting in a total of 18,834 fishing trips from 1994 to 2004 encompassing 21 taxa that account for ~94% of the annual landing.

Life History Data

Classifications of the studied taxa into life history strategies were based on by Röpke et al (in review). Röpke et al (in review) collected data on the fecundity, oocyte size, length at maturity, maximum length, and degree of parental care of each taxa (Table B.1) and sorted each taxa into three life history strategies as defined by Winemiller (1989) and Winemiller and Rose (1992).

Hydrologic data

The hydrologic variables used here were obtained from Olsen (Chapter 1) and were based on available river height data (stage) measured by the Agência Nacional de Águas at the Manacapuru station (ANA, 2016). Olsen (Chapter 1) conducted a systematic assessment of ten flood pulse variables that have the strongest relationship to catches of river-floodplain fishes and determined that three flood pulse variables, low water index two (LWI_2), maximum stage (MaxS), and high water duration (HWD), best represent flood pulse variability in the central Amazon Basin. Maximum stage (MaxS, cm) was defined as the highest water height observed during each year. Relative bankfull level was estimated based on the method used by Castello et al. (2015). The duration of high water levels were calculated as the number of days that stage was above bankfull level for high water (HWD). Low water index two (LWI_2) was calculated as the area between the stage curve and bankfull level from the time of bankfull level to the time of minimum stage. MaxS, HWD, and LWI_2 were calculated for each year between 1991 and 2004 to encompass the data range of catches with time lags of t_{-1}, t_{-2}, and t_{-3}.

Data Analysis

Flood pulse influences on multispecies catches

To address research objective one and evaluate flood pulse influences on multispecies catches overall, a total of 18 multiple linear regression models were developed. First, six models were developed to explain catch of all taxa per trip as a function of fishing effort per trip and three individual flood pulse variables (MaxS, HWD, and LWI_2) with two time lags (t_{-2} and t_{-3}). In addition to the six models created for catches of all taxa, 12 models were created using the same modeling procedure to evaluate flood pulse influences on aggregated catches of periodic and equilibrium strategists. To do this, catches of each taxa were aggregated by life history strategy and models were developed to explain aggregated catch of equilibrium or periodic taxa per trip as a function of the explanatory variables mentioned above. Fishing effort per trip was included in models to better explain catches and was calculated as the number of fishers per boat multiplied by the number of days spent fishing (fisher-days). Each flood pulse variable with associated time lag (e.g. MaxS t_{-2}, six total) was regressed individually to explain catches of all taxa per trip using the equation:

$$C_i = \beta_0 + \beta_3 E + \beta_1 S + \beta_2 R + \beta_4 Gn + \beta_5 FPV_t + \epsilon_i \qquad (1)$$

where C_i is the catch per trip at time t, E is the effort per trip expended towards catches, S is stage at time of landing (cm), R is a categorical variable to denote if water levels were rising or falling (1 for rising, 0 for falling), Gn is a categorical variable for gear (0 for seine net, 1 for gillnet), FPVt is the flood pulse variable used in each model, $\beta_0 – \beta_5$ are fitted parameters, and ε_i

is error. Available information for some of the taxa in the study area indicate that they are recruited to the fishery between 1.5 and three years after hatching (e.g. 19 months for *Prochilodus nigricans*; 33 months for *Pseudoplatystoma fasciatum*; Barthem and Fabre 2004, Isaac et al. 2016). However, only flood pulse variables of t_{-2} and t_{-3} time lags were used in this analysis because they were identified as having the strongest relationships with catches of river-floodplain fishes in the study region (Olsen Chapter 1). All flood pulse variables were scaled by their standard deviations and centered by their variable means, so that later in the analysis process they could be systematically analyzed for their relationships to catches. Catches of each trip were $\log_{10}$ transformed to satisfy the linear regression assumptions of normality and homoskedasticity. All 18 models were created using A Least Absolute Shrinkage and Selection Operator (LASSO, Tibshirani 1996) regression method with a Gaussian link function using the "glmnet" package (version 2.0-2) in R (version 3.1.2). In order to aid in the interpretation of the results, annual catches for 21 taxa were also aggregated by life history strategy and plotted to evaluate the contribution of each taxa to total catches.

To investigate flood pulse influences multispecies catches overall, flood pulse influences on catches were evaluated based on the parameter estimates associated with each flood pulse variable and associated time lags. The absolute values of parameter estimates of flood pulse variables in all taxa, periodic, and equilibrium catch models were descriptively compared and assessed for congruency.

Flood pulse influences on catches of periodic and equilibrium strategists

To address research objective two and investigate if flood pulse influences on periodic and equilibrium strategists differ, parameter estimates were used to evaluate flood pulse influences on 1) aggregated catches, and on 2) individual taxa. Flood pulse influences on aggregated catches were studied to understand the overall influences of flood pulses on catches of fishes with periodic and equilibrium life history strategies. With this approach, however, the influences of flood pulses on individual taxa would be muddled by the influences of flood pulses on catches of other taxa. Therefore, flood pulse influences on catches of individual taxa with different life histories were also investigated. The results of both analyses were then considered to determine if flood pulse influences on periodic and equilibrium strategists differ.

First, parameter estimates from the above aggregated catch models were considered to investigate flood pulse influences on catches of periodic and equilibrium strategists. To evaluate if the absolute parameter estimates in models for periodic strategists were significantly greater ($\alpha = 0.05$) than in models for equilibrium strategists, a one-sided Wilcoxon signed-ranked test (Wilcoxon 1947) was then conducted. Significantly greater parameter estimates would indicate that catches of periodic strategists are influenced by flood pulses more than equilibrium strategists.

Second, flood pulse variable parameter estimates from Olsen (Chapter 1) were used to evaluate if the strengths of flood pulse influences on individual taxa were greater for periodic or equilibrium taxa. In that study, taxa specific catches per trip for each of the 21 taxa were modeled using methods similar to equation 1, except that the model selection process could include the following additional candidate explanatory variables: number of days spent fishing, number of fishers per boat, amount of diesel used, fishing effort adjustment variables, and flood pulse variables of t_{-1} years. Additional effort variables (number of days spent fishing, number of fishers per boat, amount of diesel used) were considered as candidate variables to allow for the model selection process to choose the effort variables that best explained taxa specific catches.

Because the total (multispecies) effort of fishing trips did not always reflect the effort expended to catch each taxa, measures of total fishing effort for each trip were adjusted for each taxa specific catch based on the gears used and the proportion that each taxa contributed to the total catch of each trip. The full model used for each taxa is displayed by the equation:

$$C_i = \beta_0 + \beta_1 S + \beta_2 R + \beta_3 nD + \beta_4 nF + \beta_5 D + \beta_6 Tg + \beta_7 U + \beta_8 Ev + \beta_9 Gn + \beta_{10} FPV_1 + \beta_{11} FPV_2 + \dots \beta_{18} FPV_9 + \epsilon_i \tag{2}$$

where C_i is the $\log_{10}$ transformed catch per trip at time t (kg), S is stage at time of landing (cm), R is a categorical variable to denote if water levels were rising or falling (1 for rising, 0 for falling), nD is the number of days spent fishing, nF is the number of fishers per trip, D is the amount of diesel used per trip, Tg, U, and Ev are categorical effort adjustment variables, Gn is a categorical variable for gear (0 for seine net, 1 for gillnet), FPVs are flood pulse variables at t_{-i} years, $\beta_0 - \beta_{18}$ are fitted parameters, and ε_i is error. Explanatory variables were chosen using LASSO regression and the model selection method described in Olsen (Chapter 1).

To investigate if flood pulse influences on periodic taxa were greater than on equilibrium taxa, the strength of flood pulse influences on periodic and equilibrium taxa were evaluated. Absolute values of non-zero parameter estimates associated with each flood pulse variable in taxa specific models were compared between taxa with periodic and equilibrium life history strategies. To evaluate if absolute parameter estimates from periodic taxa specific models were significantly greater ($\alpha = 0.05$) than estimates from equilibrium taxa specific models, a one-sided Mann–Whitney U test (Mann and Whitney 1947) was conducted. Significantly greater absolute parameter estimates would provide evidence that flood pulses have greater influences on taxa with periodic life history strategies than on taxa with equilibrium life history strategies.

RDA was conducted *post hoc* to further evaluate variation in strengths and directions flood pulse influences on catches of periodic and equilibrium taxa. RDA is a multivariate constrained ordination technique where linear responses are explained as functions of environmental variables. First, annual fishing effort (fisher-days) was calculated for the study period. Before the ordination was created, annual catches for each taxa were centered by their means and scaled by their standard deviations to satisfy the RDA assumptions of multivariate normality and homogeneity of variance. Effort for each year (Et), effort of the previous year (i.e. E t_{-1}), and flood pulse variables previous years (HWD t_{-2}, MaxS t_{-2}, LWI t_{-3}) were used to explain total catch per year of each taxa. Only catches from 1995-2004 were modeled, as effort data previous to 1994 was not available. The RDA ordination was evaluated for its ability to fit data for each taxa using the goodness.cca function from the vegan package (version 2.3) in R (version 3.1.2). Finally, Monte Carlo permutation of annual catch data for each taxa (99) at $\alpha = 0.05$ was used to determine the statistical significance of the ordination.

Results

Hydrology

The study period encompassed years with extreme hydrological events (i.e. 1995, 1997, 1999) as well as normal hydrology (e.g. 1996, 2000, 2001; Figures 1.3, 2.1). MaxS was low in 1992 (1623 cm), and fluctuated between 1979 cm and 1758 cm from 1995 through 2004 (Figure 2.1a, b). HWD was also low in 1992 (169 days), high in 1994 (365 days), and fluctuated between 244 and 315 days from 1995 through 2004 (Figure 2.1c, d). LWI_2 was moderately high in 1992 (10654 units), low in 1994 (63 units), high in 1995 and 1997 (22845.5 and 22668 units, respectively), and generally decreased from 1998 through 2004 (Figure 2.1e, f). LWI_2 was the flood pulse variable that showed the most variability during the study period.

Catches of periodic and equilibrium strategists

Of the studied taxa, 17 were classified as periodic strategists and four were classified as equilibrium strategists (Table 1.1, Figure 2.2). Aggregated catches of periodic and equilibrium strategists were generally composed of a few important species. *Semaprochilodus insignis*, *Prochilodus nigricans,* and *Brycon amazonicus* dominated catches of periodic strategists (Figure 2.2a), while *Cichla spp.* and *Osteoglossum bichirrosum* dominated catches of equilibrium strategists (Figure 2.2b). Catches of periodic strategists were high in 1996 and 1999 and increased from 2001 through 2004 (Figure 2.2a), while catches of equilibrium strategists were high in 1995 and 1999 and increased from 2002 through 2004 (Figure 2.2b). Aggregated catch model accuracy was greater for periodic strategist and total catch models than for equilibrium strategist models (mean R^2 = 0.36, 0.29, and 0.09, respectively; Table 2.1).

Flood pulse influences on catches of all taxa

Flood pulse influences on multispecies catches overall appeared to be mostly influenced by relationships between flood pulses and catches of periodic strategists. Absolute parameter estimates in all taxa models for the variables LWI_2 at t_{-2}, LWI_2 at t_{-3}, and MaxS at t_{-3} were more similar in strength to parameter estimates from models of aggregated catches of periodic strategists than to parameter estimates from models of aggregated catches of equilibrium strategists (Table 2.2, Figure 2.3a). The high water flood pulse variables MaxS at t_{-2}, MaxS at t_{-3}, and HWD at t_{-2} had the strongest relationships to catches of all taxa.

Flood pulse influences on periodic and equilibrium strategists

The significance of differences of flood pulse influences on periodic and equilibrium strategists depended on the level of analysis. Absolute parameter estimates associated with flood pulse variables in aggregated catch models of periodic strategists were generally greater than in aggregated catch models of equilibrium strategists (Table 2.2, Figure 2.3). The Wilcoxon signed-ranked test showed that the absolute parameter estimates in models for periodic strategists were significantly greater than in models for equilibrium strategists, but only slightly ($p = 0.046$). For four of the six flood pulse variables tested, LWI_2 at t_{-2}, LWI_2 at t_{-3}, MaxS at t_{-2}, and HWD at t_{-2}, flood pulse influences on aggregated catches of periodic strategists were over two times stronger than on aggregated catches of equilibrium strategists (Figure 2.3, Table 2.2). The median of all absolute parameter estimates for periodic strategists was over three times greater than the median of all absolute parameter estimates for equilibrium strategists (0.008 and 0.002, respectively). Only the influences of MaxS at t_{-3} on catches of equilibrium strategists was stronger than with catches of periodic strategies (Figure 2.3a, Table 2.2). Directions of the relationships between aggregated catches and flood pulse variables were consistent among catches of periodic and equilibrium strategists, with the exception of HWD at t_{-3} (Figure 2.3a, Table 2.2).

Flood pulse influences on catches of individual taxa were greater for periodic strategists than for equilibrium strategists; median of absolute parameter values for periodic strategists was over two times greater than the median of absolute parameter values for equilibrium strategists (0.050 and 0.025, respectively). The Mann-Whitney U-test indicated that absolute parameter estimates associated with flood pulse variables in taxa specific models of periodic strategists were significantly greater than in taxa specific models equilibrium strategists ($p < 0.01$). Most taxa specific models showed positive relationships with high water flood pulse variables and negative relationships with low water flood pulse variables (e.g. *Mylossoma spp.*, Figure 1.8). However, some taxa specific models showed positive relationships between catches and low water flood pulse variables (e.g. *Colossoma macroponum* with LWI_2 at t_{-2}) and negative relationships between catches and high water flood pulse variables (*B. amazonicus* with MaxS at t_{-1}).

The RDA ordination showed that the flood pulse variables that best explained catches of each taxa varied within each life history strategy (Figure 2.4), suggesting that flood pulses can influence taxa with the same life history strategy in different ways. Taxa scores of periodic strategists on the RDA axes showed more dispersion than equilibrium strategists (Figure 2.4), which implies that the flood pulse variables that best explain catches varies more among periodic strategists than among equilibrium strategists. HWD at t_{-2} had the strongest relationships to catches of *P. nigricans* (Curimatã) and *C. macroponum* (Tambaqui), while MaxS at t_{-2} had the strongest relationships to catches of *Hypophthamlus spp.* (Mapará) and *Potamorhina spp.* (Branquinha). Overall, the RDA explained 75% of the variation in the catch data, and the first two RDA axes explained 37% and 23% of the variation in the dataset, respectively. HWD at t_{-2} was the flood pulse variable that had the greatest ability to explain catches of the 21 taxa. The RDA ordination generally explained catches of each taxa well (Table B.2), and Monte Carlo permutations showed that the RDA ordination was significant ($p < 0.05$).

Discussion

Flood pulse influences on catches of all taxa

Flood pulse influences on catches of all taxa appeared to be most influenced by flood pulse influences on periodic strategists. Catches of both periodic and equilibrium strategists were positively related to high water levels and negatively related to low water levels, with the exceptions of HWD at t_{-2} for equilibrium strategists and HWD at t_{-3} for periodic and equilibrium strategists (Table 2.2). HWD at t_{-2} and MaxS at t_{-2} were the two variables that had the strongest influence on catches of periodic strategists and catches of all taxa (Figure 2.3a), which suggests that the influences of high water levels on catches of all taxa are the strongest after a lag of two years. The direction of flood pulse relationships with catches and the two year lag of flood pulse influences on catches were consistent with other studies of the Amazon Basin which found similar high and low water influences on multispecies catches (Castello et al. 2015, Isaac et al. 2016, Olsen Chapter 1). The strong influences of high water levels on catches of all taxa could imply that flood pulses generally have strong influences on the overall recruitment and survival of all taxa in the multispecies fisheries of the Amazon Basin.

Flood pulse influences on catches of all taxa may have been most influenced by flood pulse influences on periodic strategists because periodic taxa were typically targeted more than equilibrium taxa, and as a result, made up a majority catches by weight (Figure 2.2). Fishers may have targeted a greater number of periodic taxa than equilibrium taxa because periodic strategists are generally able to rapidly increase their population sizes when environmental conditions are favorable for reproduction and growth (Winemiller 2005). For example, if higher water levels led to an abundance of *S. taeniurus*, fishers could respond by targeting that taxa more heavily. Equilibrium strategists are generally not able to rapidly increase their population sizes and may not be able to sustain stable populations if fishing pressure is high. Catches of equilibrium strategists such as *Arapaima spp.* had previously been important in local markets of the Amazon (Veríssimo 1895), but fishing pressure has reduced population sizes (Castello et al. 2011) and fishers must rely on abundant taxa that can grow to harvestable sizes quickly. Periodic strategists in the Amazon Basin also tend to exhibit schooling behavior (Goulding 1980), which allows fishers to easily target them with active gears such as seines compared to the passive gears typically used to target equilibrium taxa. These schools are mainly targeted as taxa migrate between river-channels and floodplains during rising and falling water levels (Batista and Petrere 2003).

Flood pulse influences on catches of periodic and equilibrium strategists

The medians of parameter estimates associated with flood pulse variables were two times greater for periodic strategists than for equilibrium strategists when both aggregated and taxa specific catches were analyzed (Figure 2.3a, b). Flood pulse influences on aggregated catches of periodic strategists were significantly greater than flood pulse influences on aggregated catches of equilibrium strategists at the $\alpha = 0.05$ level, but only slightly ($p = 0.046$). Flood pulse influences on catches of individual periodic taxa were significantly greater ($p < 0.01$) than flood pulse influences on catches of individual equilibrium taxa, which suggests that aggregating catches may have reduced the observed significance of the differences between flood pulse influences on catches of periodic and equilibrium strategists. Flood pulse influences on aggregated catches of periodic strategists were stronger than on aggregated catches of equilibrium strategists for all of the variables tested except MaxS at t_{-3} (Table 2.2, Figure 2.3a). This suggests that high and low water levels have greater influences on overall population fluctuations of exploited periodic taxa compared to equilibrium taxa. The strong flood pulse influences on periodic strategists support predictions from life history strategy theory (Winemiller 2005) that environmental conditions in variable ecosystems have greater influences on the recruitment of periodic strategists compared to the more consistent recruitment of equilibrium strategists.

The reduced statistical significance when aggregated catches were analyzed could have been due to the variability in the direction and time lags of flood pulse influences among catches of periodic strategists. Upon analysis of taxa specific flood pulse relationships, the RDA ordination and parameter estimates associated with taxa specific models showed considerable variability in the direction, time lags, and strengths and of flood pulse influences on catches (Figures 1.8, 2.4). For example, catches of some taxa showed strong positive relationships to HWD at t_{-2} (*C. macroponum*), while others showed weak positive relationships (*Triportheus spp.*) and weak negative relationships (*S. taeniurus*). This variability in relationships between flood pulse variables and taxa specific catches suggests that taxa with the same life history strategies may not always respond to flood pulses in the same way. Many factors could explain such variability, such as preferential targeting of certain taxa or subtle variations in the reproductive traits and behavior of taxa with the same life history. The number of periodic strategist taxa available for harvest could have allowed fishers to respond to population fluctuations by targeting taxa while they were abundant and switching to other taxa when the preferred taxa were scarce (May et al. 1979, Gulland and Garcia 1984). Decreased abundance of *C. macroponum* due to flood pulse influences could have caused fishers to target *Mylossoma spp.*, an ecologically similar but less valued taxa (Goulding 1980, Barthem and Goulding 2007, Figure 2.2a). Variations in the oocyte sizes, fecundities, and sizes at maturity among fishes with the same life history strategies could have also influenced variation in relationships between flood pulses and catches. Differences in the allocation of energy to body growth and reproductive output among ecologically similar taxa could have allowed for competitive advantages for some taxa within functional niches. Catches of two detritivorous periodic strategists that likely shared the same food resources had strong relationships to different high water flood pulse variables; catches of *P. nigricans* were more related to HWD at t_{-2}, while catches of *S. insignis* were more related MaxS at t_{-2} (Figure 2.2a). Interannual flood pulse variability could have facilitated a competitive advantage and increased the population size for *P. nigricans* when HWD was longer, while favoring *S. insignis* when MaxS was higher.

Implications

The trilateral continua of reproductive traits serves as a generalized guide of how different fishes will respond to environmental fluctuations. The results of this study are congruent with predictions of how fishes with different life history strategies respond to environmental fluctuations, and can be used to improve management of Amazonian river-floodplain populations with different life history strategies. Specific information of how high and low water levels in a given year influence taxa specific catches in future years can be used to create conservative catch quotas following interannual flood pulse variability. However, variations in the responses to flood pulses among fishes with the same life history strategies suggests that other factors could contribute to population responses to flood pulses. Given the diverse ecology of Amazonian taxa, conceptual models of how the population dynamics of fishes with different migratory behaviors or feeding strategies are influenced by different phases of flood pulses may need to be developed to accurately predict how different taxa respond to flood pulses. Fishes present in the Amazon basin possess at least three different types of migratory behavior (Barthem and Goulding 2004, Fernandes 1997, Castello 2008) and utilize floodplain habitat resources in different ways and during different times. Flood pulses are thought to alter the food resources available for different fishes throughout each year (Abujanra et al. 2009, Correa and Winemiller 2014), which could influence the growth and survival of fishes at different life stages. Only once biological relationships to resource fluctuations caused by flood pulse are fully understood can river-floodplain fishes be properly managed.

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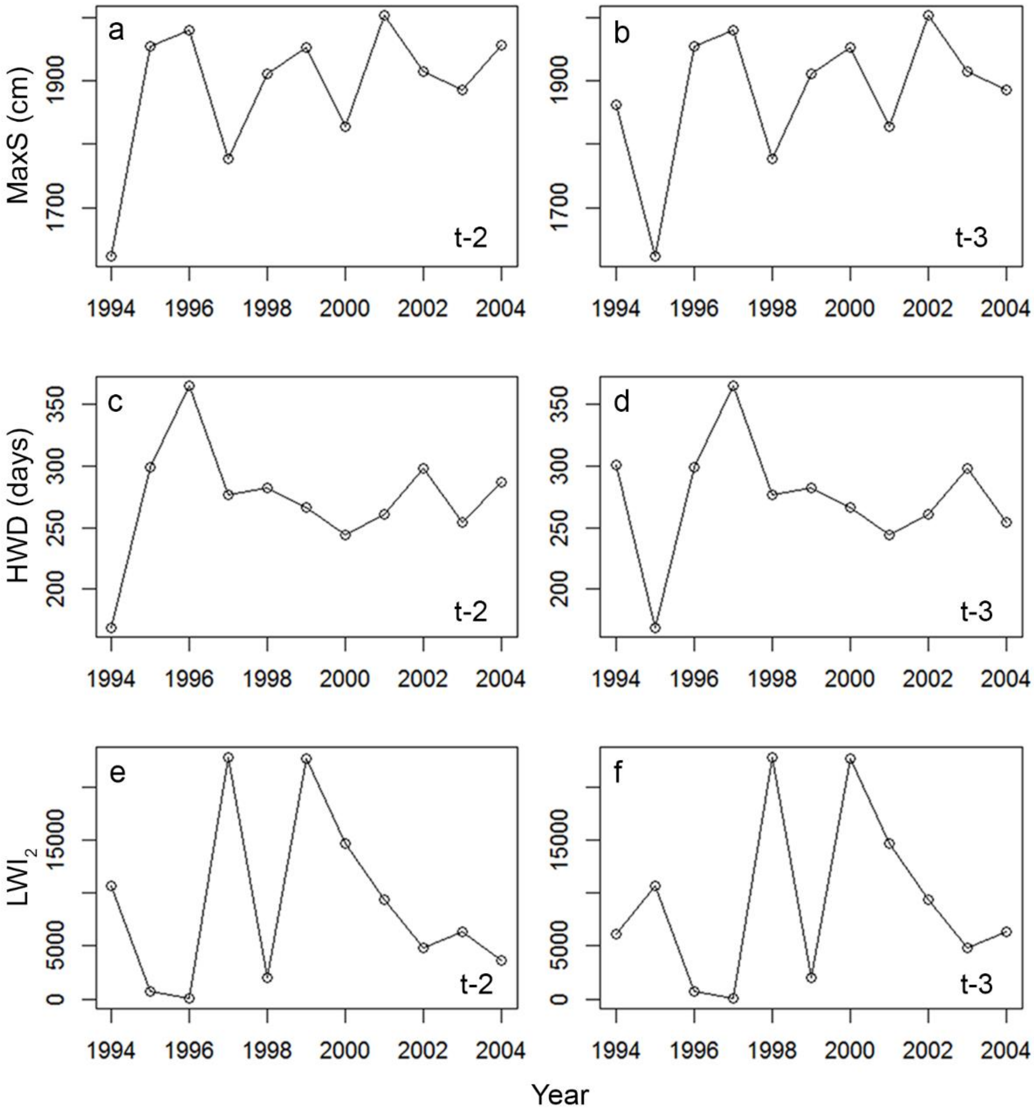

Figure 2.1. Flood pulse variable calculations of a) maximum stage (MaxS) at a lag of t_{-2} years, b) MaxS at t_{-3}, c) high water duration (HWD) at t_{-2}, d) HWD at t_{-3}, e) low water index two (LWI_2) at t_{-2}, and f) LWI_2 at t_{-3}.

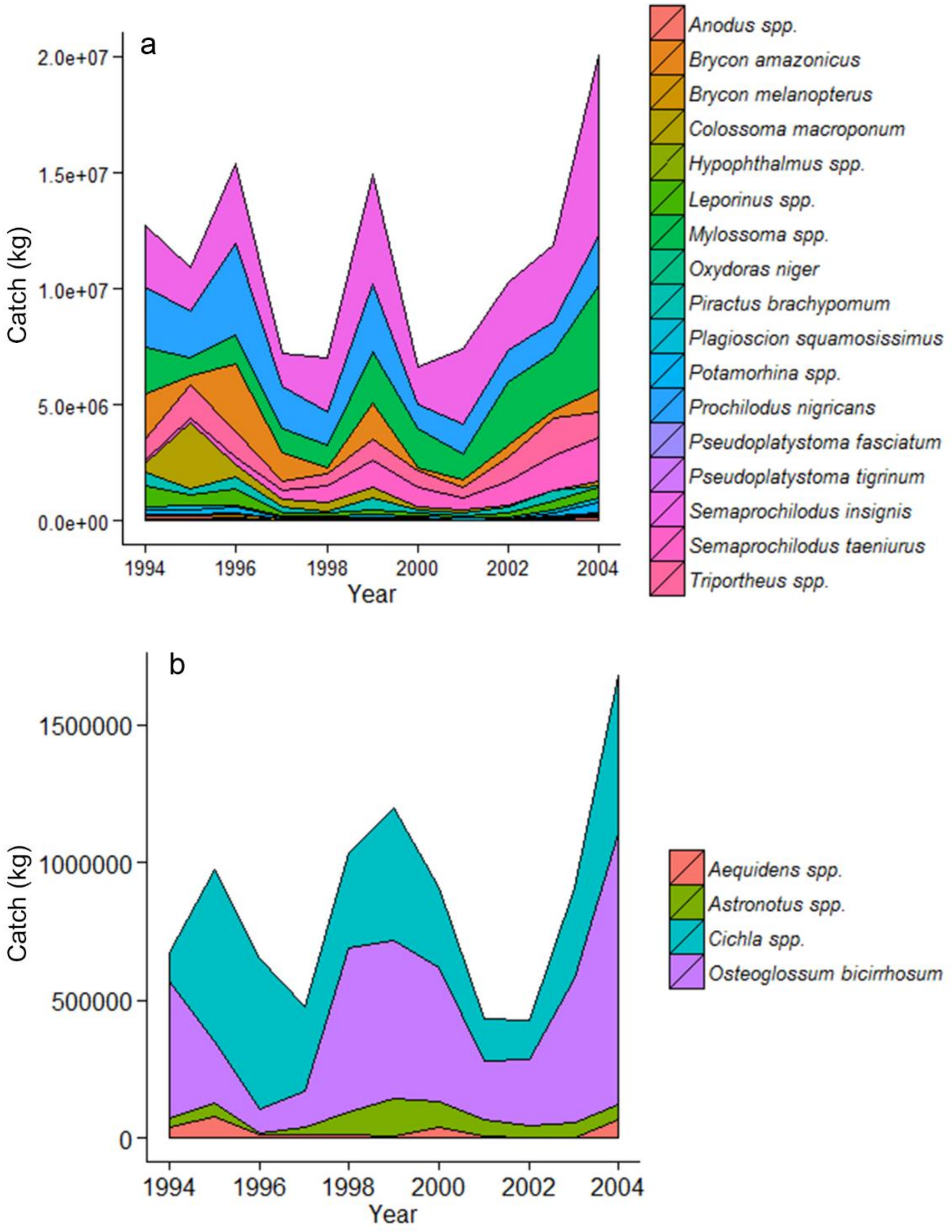

Figure 2.2. Annual catch in the Central Amazon Basin of taxa classified as a) periodic strategists and b) equilibrium strategists from 1994 through 2004.

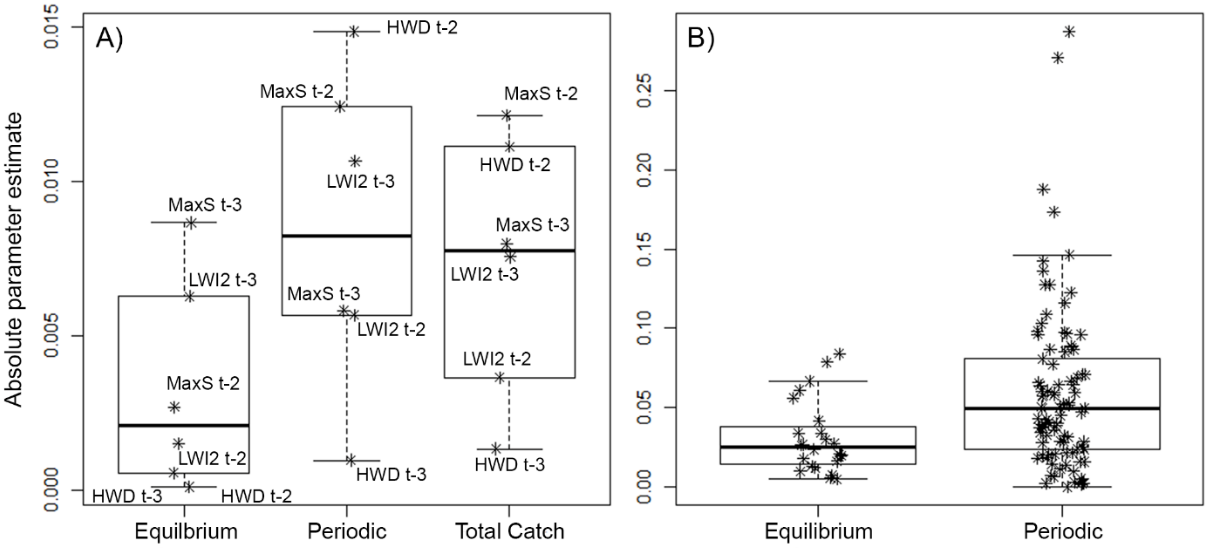

Figure 2.3. Boxplots of absolute parameter estimates associated with flood pulse variables. Data points represent absolute parameter estimates in a) total catch and aggregated catch models, and b) taxa specific models grouped by life history strategy.

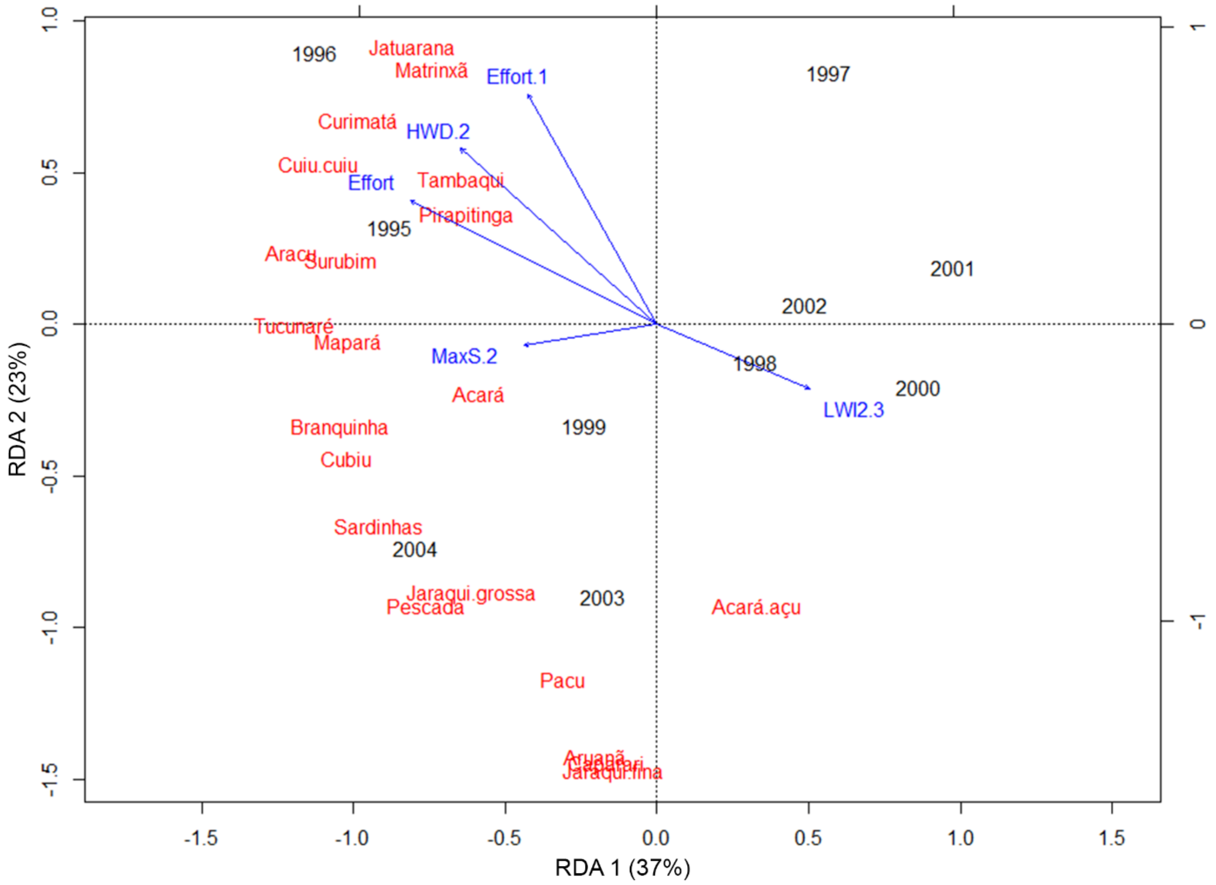

Figure 2.4. RDA biplot displaying relationships between catches of each taxa (red), explanatory variables (blue), and relationships between explanatory variables and each year in the study period (black). Perpendicular distances between taxa scores and explanatory vectors indicate how influential each variable was to explaining catches, while explanatory vector length indicates how influential each explanatory variable was to explaining catches overall. For the species represented by each common name, see Table 1.1. Percentages on x and y axes represent variance explained by each RDA axis.

Table 2.1. R^2 of models explaining catches of all taxa and aggregated catch per trip of fishes with periodic and equilibrium life history strategies as a function of effort (fisher-days), gear, seasonal flood pulse influences, and interannual flood pulse variables.

Variable	**Periodic**	**Equilibrium**	**All Taxa**
No flood pulse variables	0.34	0.09	0.28
LWI_2 t_{-2}	0.35	0.09	0.29
LWI_2 t_{-3}	0.36	0.10	0.29
MaxS t_{-2}	0.36	0.09	0.31
MaxS t_{-3}	0.35	0.10	0.29
HWD t_{-2}	0.37	0.09	0.30
HWD t_{-3}	0.34	0.09	0.28

Table 2.2. Parameter estimates of flood pulse variables when used to explain total catches and aggregated catches of fishes with periodic and equilibrium life history strategies.

Variable	Periodic	Equilibrium	All Taxa
LWI_2 t_{-2}	-5.67×10^{-3}	-1.52×10^{-3}	-3.65×10^{-3}
LWI_2 t_{-3}	-1.06×10^{-2}	-6.28×10^{-3}	-7.56×10^{-3}
MaxS t_{-2}	1.24×10^{-2}	2.70×10^{-3}	1.21×10^{-2}
MaxS t_{-3}	5.81×10^{-3}	8.66×10^{-3}	7.98×10^{-3}
HWD t_{-2}	1.48×10^{-2}	-1.20×10^{-43}	1.11×10^{-2}
HWD t_{-3}	-9.80×10^{-4}	-5.74×10^{-3}	-1.35×10^{-3}

Appendix B

Figure B.1. Annual catch of each studied taxa identified as a periodic strategist.

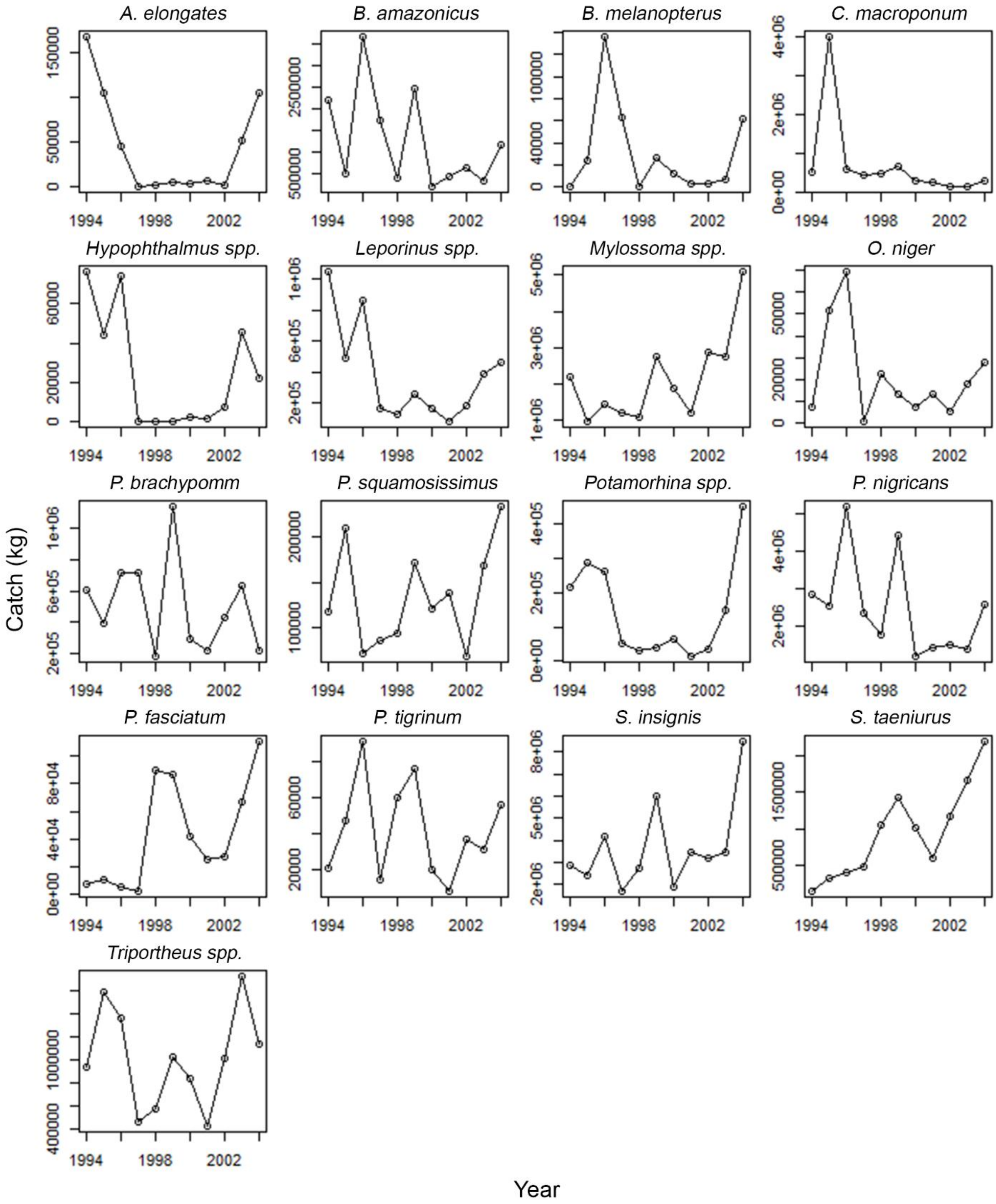

Figure B.2. Annual catch of each studied taxa identified as an equilibrium strategist.

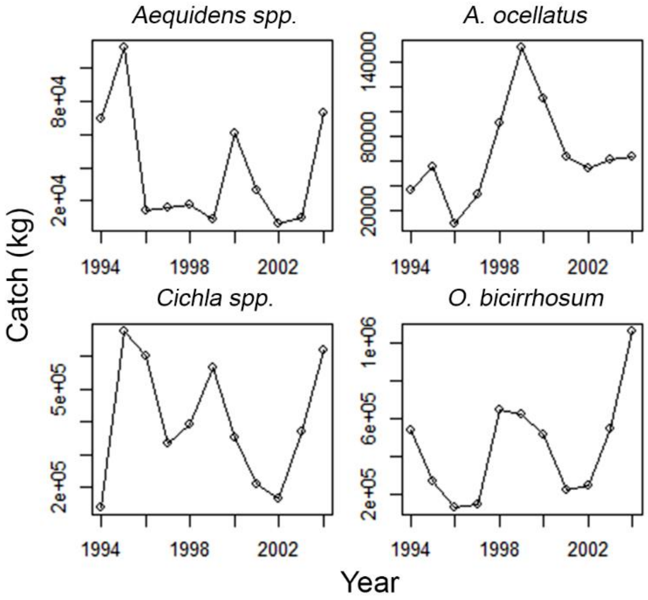

Table B.1. Reproductive and biological trait data used by Röpke et al. (in review) to classify studied taxa into life history classifications. Latin names indicate the taxa that were selected for reproductive and biological data. All measurements are in millimeters (mm). Parental care behavior for each taxa was assessed based on a scale of 1 (no parental care behavior to 6 (intensive parental care behavior).

Latin Name	Common Name	Maximum Size	Size at Maturation	Fecundity	Oocyte Size	Parental Care
Acarichthys heckelii	Acará	172	60	1340	1.7	6
Anodus elongatus	Cubiu	270	140	17300	1	0
Astronotus ocellatus	Acará-açu	250	139	2301	2.4	6
Brycon amazonicus	Matrinxã	400	320	171545	1.5	0
Brycon melanopterus	Jatuarana	400	320	171545	1.5	0
Cichla monoculus	Tucunaré	400	188	3100	2.5	6
Colossoma macropomum	Tambaqui	1000	600	1007349	1.2	0
Hypophthalmus edentatus	Mapará	360	240	64171	1	0
Leporinus friderici	Aracu	330	141	28950	1	0
Mylossoma duriventre	Pacu	220	124	25500	1.3	0
Osteoglossum bicirrhosum	Aruanã	560	477	310	12	4
Oxidoras niger	Cuiu-cuiu	1000	405	114855	1	0
Piaractus brachypomum	Pirapitinga	800	34.9	887654	1.1	0
Plagioscion squamosissimus	Pescada	360	188	15991	0.6	0
Potamorhina altamazonica	Branquinha	250	129	74227	1	0
Prochilodus nigricans	Curimatá	300	177	69427.3	1	0
Pseudoplatystoma fasciatum	Surubim	1000	410	202960	1	0
Pseudoplatystoma tigrinum	Caparari	600	410	202960	1	0
Pygocentrus nattereri	Piranhas	340	172	5900	2	2
Semaprochilodus insignis	Jaraqui-grossa	300	202	81070	1	0
Semaprochilodus taeniurus	Jaraqui-fina	300	164	81070	1	0
Triportheus angulatus	Sardinhas	250	89	20634	1	0

Table B.2. Proportion of constrained variance explained by RDA axes and unconstrained variance explained by Principal Component (PC) axes.

	RDA1	**RDA2**	**RDA3**	**RDA4**	**RDA5**	**PC1**	**PC2**	**PC3**	**PC4**
Eigenvalue	7.84	4.80	2.23	0.60	0.28	2.20	2.07	0.69	0.29
Proportion Explained	0.37	0.23	0.11	0.03	0.01	0.10	0.10	0.03	0.01
Cumulative Proportion	0.37	0.60	0.71	0.74	0.75	0.85	0.95	0.99	1.00

Conclusions

Studying the influences of natural river-floodplain hydrology on diverse fish populations has provided knowledge that can further the implementation of ecosystem based management in degraded river-floodplain ecosystems. My research is congruent with other studies of the Amazon that studied flood pulse influences on multispecies catches using different datasets (Merona and Gascuel 1993, Castello et al. 2015, Isaac et al. 2016): high water levels were generally related to increased catches two to three years later, while low water levels were generally related to decreases in catches two to three years later.

My research may support the theory that flood pulses have the greatest influence on fish populations in the Amazon Basin during larval and juvenile life stages (Isaac et al. 2016). Isaac et al. (2016) hypothesized that flood pulses in the Amazon Basin have the greatest influences on larval fishes after finding that the mean age at catch was similar to the lag of flood pulse effects on catches. Most commercially important taxa in the Amazon Basin are periodic strategists, whose juvenile survival and growth are thought to be strongly influenced the environmental conditions present at the time of hatching (Winemiller 2005). Catches of periodic strategists were most related to high water flood pulse variables after lags of two years, which are roughly similar to the age of most periodic strategists at the time that they are recruited to the fishery (Isaac et al. 2016). My research therefore suggests that flood pulses generally have strong influences on the overall recruitment and survival of juvenile fishes in multispecies fisheries of the Amazon Basin, and may have the greatest influence on fish populations in the Amazon Basin during larval and juvenile life stages.

Collinearity was observed among the ten candidate flood pulse variables selected to test for flood pulse influences on fish taxa. Three dimensions were identified as being able to explain 97% of the variability of Amazonian flood pulses and matched three flood pulse variable measurements, MaxS, HWD, and LWI_2. This could indicate that the three most important measures of unimodal flood pulses in large river-floodplains are 1) how high water levels rise, 2) how long and severe low water levels are, and 3) how long high water levels are relative to low water levels. The maximum height of high water levels dictates the amount of inundated floodplain area that can be utilized by fishes, while the minimum height dictates how confined and susceptible fish populations are to increased natural and fishing mortality rates. The duration of high water levels would account for how long fishes can utilize floodplain food, shelter, and reproductive resources. Although flood pulse patterns may be different in other river-floodplain ecosystems, representing these three dimensions is important when determining the different variables used to describe natural unimodal flood pulses.

Flood pulse influences on catches of all taxa in the Amazon Basin were likely driven by fishers targeting mainly periodic strategists, given that they were influenced by flood pulses more than equilibrium strategists and that they ultimately made up a majority catches by weight. The variety of periodic taxa that fishers could target could have reduced the fishing pressure on any one taxa of periodic strategist at a given time. The diversification of catches in response to differences in abundant taxa would allow populations of different periodic strategists time to recover from fishing pressure, while fishers could target other abundant taxa and still maintain a high level of catches of periodic strategists overall (Gulland and Garcia 1984).

Variability was observed within each life history strategy in the flood pulse variables and time lags that were most related to catches of each taxa. Flood pulse influences on taxa did not always conform to general expectations that high water levels increase catches, and low water levels decrease catches; catches of some taxa were negatively related to high water levels and positively related to low water levels. Differences in the influences of flood pulses among taxa with the same life history strategies may have been related to other biological or ecological aspects specific to each taxa, such as subtle differences in reproductive biology, differences in feeding strategies, or differences in migratory behavior.

Overall, my research can be used to better understand flood pulse influences on taxa with different life history strategies, and can facilitate the creation of flexible catch quotas based on the flood pulse measurements. Management of tropical river-floodplain should incorporate measures of both high and low water levels of previous years when determining catch regulations for a given year. Two to three years after greater and longer high water levels, catch quotas in the Amazon Basin can be more liberal given that most taxa should have greater juvenile survival and thus fishery recruitment. Two to three years after longer and severe low water levels, catches quotas in the Amazon Basin should be more conservative, given that the juvenile survival and thus fishery recruitment would be low due to predation and hypoxia induced natural mortality. Taxa specific information on how flood pulse variables in a given year can influence catches of diverse taxa in future years could be used to refine taxa specific management of Amazonian river-floodplain populations. Given the feeding and migratory behaviors present among commercially important taxa in the Amazon Basin, future studies could investigate how biological traits of individual taxa could further explain variability in the population response to flood pulses. Understanding of ecological relationships to catches is paramount to the proper management of fish populations in seasonal environments.

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