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RESEARCH ARTICLE

Hydrological controls of fisheries production in a major Amazonian tributary

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Abstract

Amazonian rivers are characterized by a strongly seasonal flood pulse, which is being altered by ongoing and planned hydropower development across the basin. Changes in hydrology have a cascade of physical, ecological, and social effects, and some ecohydrological changes in the Amazon are expected to be irreversible. To better understand these linkages, we investigated shared trends and causal factors driving fish catch in a major Amazonian tributary before dam construction to derive relationships between catch and natural hydrologic dynamics that can be used to assess likely post-dam fisheries impacts. We applied a time series-based dimension reduction technique (dynamic factor analysis) to investigate dynamics in fish catch across 10 commercially important species using daily fish landings and hydrological data. We found a 4-trend dynamic factor model to best fit the observed data, with fitted trends exhibiting variation representative of seasonal and longer-term hydrologic variation. We next considered 11 candidate explanatory time series and found the best dynamic factor model used 4 explanatory variables: maximum water level, flooding duration, previous year's flow, and rate of change in flow; however, each species showed a unique response to this set of hydrological variables. Species-specific responses suggested that future dam operating rules need to closely mimic the natural hydrologic regime in order to maintain the biological dynamics of this and similarly diverse systems. In particular, high flows associated with increased catch the following year are important to maintain, but may be difficult to achieve in the context of reservoir regulation and energy production goals.

KEYWORDS

Amazon, artisinal fishery, dams, hydropower, time series analysis

1 | INTRODUCTION

The 6 million-km^2 Amazon River watershed (Figure 1) is the world's largest river basin and is widely recognized as one of the planet's most vital natural and cultural resources. Water quantity and quality in the Amazon and its many tributaries integrate the myriad biophysical and anthropogenic processes that occur within the basin (Coe, Costa, & Soares-Filho, 2009) and provide the foundation for many of the system's ecosystem services, which are valued at a minimum of US $30 billion per year (Butler, 2009). The magnitude and timing of flow in Amazonian river systems and their associated lakes and wetlands are characterized by a strongly seasonal flood pulse (Junk, Bayley, & Sparks, 1989). Many studies have elucidated how the flood pulse promotes high primary and secondary production in the Amazon and other tropical rivers, with some of the most important effects observed in the dynamics of fish stocks and fishing yields (Bayley, 1995;

Castello, Isaac, & Thapa, 2015; Fearnside, 2013; Górski et al., 2012; Halls & Welcomme, 2004; Isaac, Castello, Santos, & Ruffino, 2016; Mérona & Gascuel, 1993; Moses, 1987; Petesse & Petrere, 2012). Beyond the scientific community, fishermen also recognize important associations between hydrological dynamics, fishing efficiency, and economic earnings (Doria, Lima, & Neto, 2015; Gonçalves & Batista, 2008; Isaac & Cerdeira, 2004).

The Amazon is also a relatively untapped source of renewable energy for Latin American countries reliant on hydropower for electricity. Construction of 243 hydroelectric dams across the Amazon is underway as a result of government plans geared toward increased energy security, economic growth, improved living standards, and industrialization (Lees, Peres, Fearnside, Schneider, & Zuanon, 2016; Soares-Filho et al., 2006). Changes in the Amazon's freshwater ecosystems from hydropower development will have a cascade of physical, ecological, and social effects; impacts on fish and fisheries from
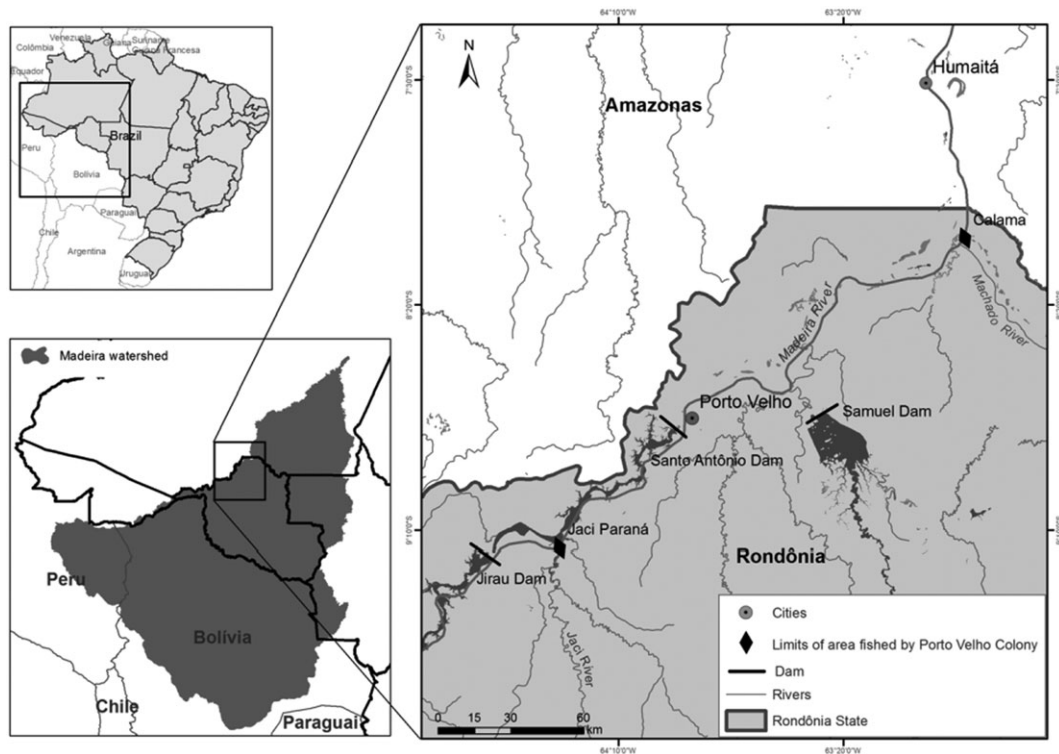
FIGURE 1 Geographic location of the study area, with insets showing the transnational Madeira River basin and the extent of the river fished by the Porto Velho fishermen's colony

changes in water quantity, quality, and timing are expected to be particularly deleterious (Agostinho, Pelicice, & Gomes, 2008; Tundisi, 1990) and potentially irreversible (Gubiani, Angelini, Vieira, Gomes, & Agostinho, 2011). These changes can create substantial and wide-ranging social impacts in communities that have historically depended on small-scale fisheries for subsistence and economic stability (Fearnside, 2013).

Small-scale fisheries are characterized as low-cost, family-based enterprises that use simple fishing fleets for short fishing expeditions (FAO, 2014). Small-scale fisheries employ 90% of the world's fishermen and contribute approximately half of all global fish catch (86.6 million t in 2012). These local fisheries are critical for food security, with catches used primarily for subsistence as an important source of protein and for local income (FAO, 2014). In the Brazilian Amazon, small-scale fisheries employ over 175,000 workers (Ruffino, 2014), with an estimated production of nearly 140,000 t (Ministério da Pesca e Aquicultura [MPA], 2010) worth approximately US$278 million annually (Almeida, Lorenzen, & McGrath, 2004). Fish are also the main food resource for the most riverine communities (Isaac et al., 2015), where fish consumption was estimated at 169 kg per person per year, one of the highest rates in the world. Technological improvements, growth of regional markets, increasing export demand, and an increasing number of fishermen have also contributed to the strong socioeconomic dependence on fisheries among Amazonian riverine communities (Almeida, Mcgrath, & Ruffino, 2001). Ongoing and planned expansion of hydropower development in these tightly coupled social-ecological systems (e.g., Epstein, Vogt, Mincey, Cox, & Fischer, 2013; Ostrom, 2009) requires an improved

understanding of trends and causal factors affecting fisheries production in both dammed and undammed systems.

Flow variability is widely recognized as a primary driver of biotic and abiotic conditions in riverine systems (Naiman, Latterell, Pettit, & Olden, 2008; Poff et al., 1997; Richter, Baumgartner, Powell, & Braun, 1996). In addition to longitudinal and lateral connectivity (Junk et al., 1989; Vannote, Minshall, Cummins, Sedell, & Cushing, 1980), maintenance of a "natural" flow regime is critical for sustaining healthy riverine ecosystems and the services they provide (Acreman et al., 2014; Gilvear, Spray, & Casas-Mulet, 2013; Loomis, Kent, Strange, Fausch, & Covich, 2000). The flood pulse concept (Junk et al., 1989) predicts that more periodic pulsing is associated with increased productivity, biodiversity and species adaptation (Junk & Wantzen, 2004), and dynamic river-floodplain environments such as the Amazon, Mekong, Congo, and Yangtze Rivers and their large tributaries have some of the highest levels of biodiversity and productivity in the world (Fitzhugh & Vogel, 2010; Fu, Wu, Chen, Wu, & Lei, 2003; Mérona & Rankin-de-Mérona, 2004; Winemiller et al., 2016; Ziv, Baran, Nam, Rodriguez-Iturbe, & Levin, 2012). In this context, understanding how the flood pulse and other elements of the flow regime affect fisheries production in the Amazonian in the absence of dams is important for predicting likely impacts of ongoing and future dam construction.

For fish, the hydrological cycle is a primary regulatory component of the ecosystem, influencing reproduction, migration, growth, and food availability (Agostinho, Gomes, Veríssimo, & Okada, 2004; Isaac, Almeida, Cruz, & Nunez, 2015; Vazzoler, 1996). For example, fish reproduction in tropical rivers is characterized by a cyclic process

related to hydrologic variation (Agostinho, Vazzoler, Gomes, & Okada, 1993), whereby fish time their spawning with the flood pulse to utilize floodplains for feeding and rearing (Fitzhugh & Vogel, 2010). Floodplains promote favourable environments for protection, feeding, and reproduction, where species feed during high water level and conserve energy during the dry season for reproductive success (Bunn & Arthington, 2002; Welcomme, 1985). In the Amazon, many fish species reproduce during the rising limb and maximum flood stages, which guarantees fry shelter, protection, and food until they reach the juvenile stage (Barthem & Fabré, 2004; Vazzoler, 1996) and return to the main channel when waters recede (Arantes, Castello, Cetra, & Schilling, 2013). Another significant factor in the Amazon is hydrologic connectivity of freshwater ecosystems, especially between the Andes and Amazonian floodplain (Finer & Jenkins, 2012), which provides for dispersal and colonization of species in periods of low and high water (Hurd et al., 2016; Torrente-Vilara, Zuanon, Leprieur, Oberdorff, & Tedesco, 2011).

Following from its role in structuring fish reproduction, migration, and growth, the flood pulse has also been shown to play a major role in the dynamics of fishing yields (Bayley, 1995; Castello et al., 2015; Fearnside, 2013; Halls & Welcomme, 2004; Petesse & Petrere, 2012). In addition to directly affecting fish abundance, seasonal changes in water level and fish habitat also affect catchability and fishing effort (Isaac et al., 2016). Fishermen recognize hydrological variations and the responses of associated species and use this knowledge to maximize fishing performance by targeting different species throughout the year (Isaac et al., 2016). For example, years after intense flood events are usually more profitable because high waters promote increased connection with habitats for feeding, decreasing natural mortality and predation, and increasing recruitment in future years (Welcomme & Halls, 2004). Conversely, periods with low water, in addition to increasing natural mortality, favour fishing activities (Welcomme, 1985).

Many authors have used models to demonstrate the importance of hydrologic seasonality in different aspects of fish community dynamics and interactions, including the influence of floods on species assemblages, reproduction, and recruitment of some species (Agostinho et al., 2004; Jiménez-Segura, Palacio, & Leite, 2010). Approaches include model simulation experiments using time series data and variation in hydrological conditions (Agostinho et al., 2004; Erzini, Inejih, & Stobberup, 2005; Goto et al., 2015; Jiménez-Segura et al., 2010); modelling of regulatory processes affecting abundance, biomass, and spatiotemporal variations of fish populations (Hossain, Gopal Das, Sarker, & Rahaman, 2012; Silva, de Oliveira Pereira, Vieira, & Petry, 2013; Sousa & Freitas, 2008); conceptual models to evaluate interactions between fishing, fish, and seasonal flooding (Mosepele, Moyle, Merron, Purkey, & Mosepele, 2009); and analysis of the effects and integration of fisheries exploitation and environmental conditions on the ecological indicators in different marine ecosystems (Corrales et al., 2015; Fu et al., 2015).

Several studies have shown strong relationship between fisheries and elements of the hydrological regime in riverine ecosystems around the world (e.g., Górski et al., 2012; Moses, 1987). In the Amazon, a number of authors have linked hydrological variables with Amazonian fish and fisheries. For example, Mérona and Gascuel (1993) and

Matthews and Marsh-Matthews (2003) used primarily linear models to demonstrate flood pulse effects on fish catch across species, highlighting positive associations between the flood peak and species recruitment, as well as an increase in natural mortality during severe low-water levels that affected catch up to 2 years later. Other studies have stressed the maintenance of channel-floodplain connectivity as a major factor controlling the diversity and resilience of migratory and nonmigratory fish species (Welcomme, 1995). Castello et al. (2013, 2015) modelled the connections between fisheries, flooding, and effort, concluding that the magnitude and timing of low- and high-water periods, when combined with fishing effort, explained most of the observed interannual variability in fisheries yields. In a recent study, Isaac et al. (2016) expanded upon these insights by also considering fishing gear and catchability to show how fishermen alternate habitats and species to optimize their economic and biomass returns; this study also identified important water level lag effects, indicating that extremely wet years led to increased fisheries recruitment in later months and years.

In this work, we aim to build on this foundation of fisheries ecohydrology and modelling by leveraging one of the few long-term fisheries catch records available in the region. Data in this study come from the Madeira River (Figure 1), a major tributary of the Amazon. The Madeira contributes approximately 4% of the total Amazonian fish catch (Barthem & Goulding, 2007) and was recently recognized for having the greatest wealth of fish species (>1,000) in the world (Ohara et al., 2015). The Madeira River watershed is also central to the Brazilian government's hydroelectric energy development plans (Plano Decenal de Expansão de Energia; Decadal Energy Expansion Plan; Brasil, 2011). Construction of the Santo Antônio and Jirau dams (Figure 1) was completed in 2011 and 2012, respectively, creating two new reservoirs and extinguishing two main rapids, the Santo Antônio and Teotônio falls. Here, we focus on long-term fish catch records from before dam construction to better understand shared temporal trends among fish species and to derive relationships between catch and natural hydrologic dynamics characterized by a strong seasonal flood pulse. This analysis thus provides a critical baseline for the magnitude and variation in fisheries catch before disturbance of this regime by dam construction and operation.

Long-term biological monitoring is useful for characterizing the ranges and temporal variation of fisheries catch and supporting the development of relationships among potential predictor variables (e.g., Castello et al., 2013; Castello et al., 2015; Isaac et al., 2016). However, investigating relationships between multivariate time series to improve understanding of system dynamics using visual inspection and comparative statistics is difficult, subjective, and may not appropriately characterize the system (Ritter, Regalado, & Muñoz-Carpena, 2009). Nevertheless, a better understanding of biological and ecohydrological dynamics is vital to the development of management scenarios to protect valued natural resources, especially in the face of acute anthropogenic modification. In this context, an alternative approach for identifying common trends and causal factors from complex and heterogeneous data is required. To address this challenge, we applied dynamic factor analysis (DFA), a multivariate times series dimension reduction technique, to investigate intra-annual

and interannual dynamics and long-term trends in fish catch across the 10 most abundant fish species in the Madeira River, which represent over 80% of the total recorded landings by mass. DFA seeks to model observed time series (response variables) as linear combinations of one or more common trends (representing unexplained variability) and zero or more explanatory variables (representing explained variability) (Zuur, Tuck, & Bailey, 2003). Modelling time series data as a combination of common trends and explanatory variables is useful for analysing relationships among the components of complex environmental systems, where DFA can help reveal associations among response variables and identify which explanatory variables (if any) most affect the time series of interest. By quantifying specific links between fish catch and hydrology, we aim to provide guidance for future dam operation that best supports the region's important fisheries resource and remarkable biological diversity.

2 | MATERIAL AND METHODS

2.1 | Study area

The Madeira River (Figure 1) drains over 1.4 million km^2 in Brazil, Bolivia, and Peru and is one of the most important Amazonian tributaries in terms of flow and sediment delivery to the Amazon River (Latrubesse, Stevaux, & Sinha, 2005; Siqueira Júnior, Tomasella, & Rodriguez, 2015). Flow in the Madeira River is strongly seasonal, with average discharge measured at Porto Velho (Figure 1) varying between 5,000 and 35,000 m^3 s^{-1} in the peak dry and wet seasons, respectively (Figure 3). The main branch of the Madeira is characterized by 19 major rapids, some of which are important as geographical barriers to migration and fish distribution (Goulding, Barthem, & Ferreira, 2003; Siqueira Júnior et al., 2015; Torrente-Vilara et al., 2011). Importantly, the Madeira River currently has two operational dams, the Jirau and Santo Antônio (Figure 1); however, their construction began in 2008, after the data presented here were collected. In Brazil, the Madeira River runs through the state of Rondônia. The vast majority of the Madeira River fish catch in Rondônia (755 ± 315 t year^{-1}; Doria, Ruffino, Hijazi, & Cruz, 2012) is landed at the Porto Velho fish market (Cai N'água), which is managed by the "Z-1" Fishermen's Colony, a loose association of independent fishermen in the city of Porto Velho and 12 nearby districts (Instituto Brasileiro de Geografia e Estatística, 2010). The Colony represents approximately 70 riverine communities, totalling 1,522 associated fishermen. Fishermen in the region use simple fishing fleets consisting of small wooden boats, and fishing expeditions typically involve a few fishermen per craft on short, low-cost trips. Fishermen use a variety of handmade gear (e.g., gill nets, harpoon, and cast net), and their catch is intended primarily for the local market (Doria et al., 2012).

2.2 | Fisheries and hydrological data

The Z-1 Fishermen's Colony recorded daily fish landings at the Cai N'água fish market, including species and total landed weight (kilogram). The Z-1 Colony kindly provided these data to our group at the Laboratory of Ichthyology and Fisheries at the Federal University of Rondônia. Taxonomic identification of fish was confirmed to the species level when possible following Queiroz et al. (2013). In this work, daily data were aggregated to the monthly sums for analysis, and we focused on the 10 most abundant fish (by mass) represented in the dataset: *Prochilodus nigricans* (curimatã), *Brachyplatystoma* spp. (dourada/filhote), *Mylossoma* spp. (pacu), *Semaprochilodus* spp. (jaraqui), *Brycon* spp. (jatuarana), *Triportheus* spp. (sardinha), *Potamorhina* spp. (branquinha), *Pseudoplatystoma* spp. (surubim), *Schizodon* spp. (piau), and *Cichla pleiozona* (tucunaré). Although effort is a fundamental component of understanding fisheries production (Castello et al., 2015), effort data for this small-scale fishery were not available, and we used landings across species as our response variables in the analyses described below.

Daily hydrological data were obtained with the Mineral Resources Research Company (Companhia de Pesquisa de Recursos Minerais) monitoring station located in Porto Velho. Data included discharge (cubic metre per second) and water level (metres above sea level; masl). These data were aggregated to monthly averages and used to calculate minimum, maximum, and mean monthly values for flow and level; monthly flow increment (i.e., month-to-month change in discharge); and the number of days per month the river was flooded above a critical stage (16 masl, which was identified as an important hydrologic indicator of increased fisheries production by members of the Z-1 Colony; Doria et al., 2015).

2.3 | Dynamic factor analysis

Dynamic factor analysis is a parameter optimization and dimension reduction technique that can be applied to identify interactions between a set of response variables and possible explanatory factors (Zuur et al., 2003). DFA seeks to identify parsimonious, statistical time series models (dynamic factor models; DFMs) that model observed data as linear combinations of common trends and explanatory variables. Common trends represent shared, but unexplained (i.e., latent), variation among response variables, whereas explanatory variables represent known variability correlated with response variable dynamics. The goal of DFA is to identify one or more common trends that represent latent variation shared among response variables and to minimize the number of trends required to achieve an acceptable model fit to measured data. Appropriate explanatory variables may improve the model fit, remove reliance on common trends, and identify external that affect the response variables, thus improving conceptualization of the system that drives variation in the response variables.

Initially developed for analysis of economic models (Engle & Watson, 1981; Geweke, 1977), DFA has more recently been applied to better understand a variety of physical and biological processes, from commercial fisheries production (Begoña Santos et al., 2012; Erzini et al., 2005; Pérez-Rodríguez, 2012; Scarcella et al., 2015; Zuur & Pierce, 2004), to groundwater and soil moisture dynamics (Kaplan & Muñoz-Carpena, 2011, 2014; Kaplan, Muñoz-Carpena, & Ritter, 2010; Kovács, Márkus, & Gábor, 2004; Ritter & Muñoz-Carpena, 2006), to large-scale variation in rainfall and vegetation cover (Campo-Bescós et al., 2013; Kuo, Chu, Pan, & Yu, 2011), and links between long-term climate and tree growth (Linares & Camarero, 2012; Linares & Tíscar, 2011).

With DFA, temporal variation in a set of N observed time series is modelled as a linear combination of one to M common trends, zero to K explanatory variables, a constant intercept parameter, and noise (Zuur et al., 2003):

$$s_n(t) = \sum_{m=1}^{M} \gamma_{m,n} \alpha_m(t) + \mu_n + \sum_{k=1}^{k} \beta_{k,n} v_k(t) + \varepsilon_n(t), \quad (1)$$

$$\alpha_m(t) = \alpha_m(t\text{-}1) + \eta_m(t), \quad (2)$$

where $s_n(t)$ is a vector containing the set of N response variable time series (in this case, monthly fish landings across ten species [kilogram]); $\alpha_m(t)$, same units as response variables, is a vector containing the common trends; $\gamma_{m,n}$ (dimensionless) are weighting coefficients ("factor loadings") representing the relative importance of each common trends to each response variable; μ_n (same units as response variables) is a constant level parameter (usually insignificant or zero when using normalized time series); $v_k(t)$, units vary, is a vector containing the explanatory variables (see below); and $\beta_{k,n}$ (units variable) are weighting coefficients ("regression parameters") for the explanatory variables that indicate the relative importance of each explanatory variable to each response variable. The terms $_n(t)$ and $\eta_m(t)$, same units as response variables, are independent, Gaussian noise with zero mean and unknown diagonal or symmetric, non-diagonal covariance matrix.

Common trends are modelled as a random walk (Harvey, 1989) and predicted with a Kalman filter/smoothing algorithm and expectation maximization techniques (Dempster, Laird, & Rubim, 1977; Shumway & Stoffer, 1982; Wu, Pai, & Hosking, 1996). Factor loadings ($\gamma_{m,n}$) and level parameters (μ_n) are also estimated using the expectation maximization technique, whereas simple linear regression is used to estimate regression parameters ($\beta_{k,n}$; Zuur & Pierce, 2004). Calculated values of $\gamma_{m,n}$ and $\beta_{k,n}$ are used to characterize the magnitude and direction of relationships among response variables and common trends ($\gamma_{m,n}$) and explanatory variables ($\beta_{k,n}$). Estimated $\beta_{k,n}$ with t values >2 were considered to be significant (Ritter et al., 2009). Canonical correlation coefficients ($\rho_{m,n}$) was used to quantify relationships between response variables and common trends, with $\rho_{m,n}$ close to one indicating a high degree of association. We classified the strength of these correlations into four groups: "minor" ($|\rho_{m,n}| < 0.25$); "low" ($0.25 \leq |\rho_{m,n}| < 0.50$); "moderate" ($0.50 \leq |\rho_{m,n}| < 0.75$); and "high" correlations ($|\rho_{m,n}| \geq 0.75$; Ritter et al., 2009).

2.4 | Explanatory variables

We explored 11 candidate explanatory hydrological variables for inclusion in this analysis (Table 1), including mean, maximum, and minimum monthly water level in the current year (WL_{avg}, WL_{max}, and WL_{min}); mean, maximum, and minimum monthly water level in the previous year ($WL_{avg,y-1}$, $WL_{max,y-1}$, and $WL_{min,y-1}$); number of days when the water level exceeded 16 masl in the current ($Days_{flooded}$) and previous ($Days_{flooded,y-1}$) years; Madeira River flow in the current (Q) and previous (Q_{y-1}) years; and the monthly flow increment (i.e., month-to-month change in discharge).

In addition to investigating contemporaneous association between fish landings and hydrological variables (Castello et al., 2015; Erzini,

TABLE 1 Time series variables used in the dynamic factor analysis

Variables	Series type	Description
Landings	Response	Monthly landings (kilogram) for each of the 10 highest-abundance fish species recorded at the Porto Velho fish market
WL_{avg}	Explanatory	Mean, maximum, and minimum monthly water level (masl) in the Madeira River at Porto Velho in the current year
WL_{max}		
WL_{min}		
$WL_{avg,y-1}$		Mean, maximum, and minimum monthly water level (masl) measured in the Madeira River at Porto Velho in the previous years
$WL_{max,y-1}$		
$WL_{min,y-1}$		
$Days_{flooded}$		Number of days in a month when the water level exceeded 16 masl in the current and previous year
$Days_{flooded,y-1}$		
Q		Madeira River flow ($m^3 s^{-1}$) in the current and previous years
Q_{y-1}		
Increment		Monthly change in flow

2005), there are also potentially time lags between hydrological drivers and impacts on fisheries production (Castello et al., 2015; Mérona & Gascuel, 1993). We incorporated the potential for this lag in two ways: (a) through the explicit inclusion of hydrologic variables lagged by 1 year in the DFA (shown in Table 1); and (b) via a cross-correlation analysis (CCA) between response and explanatory variables lagged between 0 and 24 months performed using R statistical software (R Core Development Team, 2016). Although the CCA identified a number of significant lags between specific fish species and explanatory variables (see Section 3), they neither were consistent across species or variables, nor did they improve overall model performance relative to unlagged and 1-year-lagged variables. Because the goal of this work was to identify patterns of shared variation among different species using the most parsimonious model, specific monthly lags for each variable/species combination were not included as potential explanatory variables. However, the CCA results were used to help explain the magnitude and sign of the regression parameters for the explanatory variables that were included. Finally, because multicollinearity may exist between variables with similar time series structure, not all candidate explanatory variables could be used simultaneously. To assess the severity of multicollinearity, we used the variance inflation factor (VIF) of each set of potential explanatory variables (Zuur, Ieno, & Smith, 2007) and excluded combinations with VIF > 5 (Ritter et al., 2009).

2.5 | Analysis procedure

We implemented DFA in three distinct steps, resulting in three models (Table 2). Model I was developed by building a set of DFMs using an increasing number of common trends until model performance was deemed satisfactory according to goodness-of-fit indicators (Zuur et al., 2003). DFM goodness of fit was quantified with Akaike's

TABLE 2 Dynamic factor models (DFM) tested in this study

DFM	No. of trends	Explanatory variables	Regression parameters	No. of parameters	AIC	R^2
Model I	4	—	—	54	4097.9	0.51
Model II	1	WL_{max}, $Days_{flooded}$, Q_{y-1}, and increment	From DFA	70	4053.9	0.31
Model IIIa	0	WL_{max}, $Days_{flooded}$, Q_{y-1}, and increment	From R	50	−88.65	0.22
Model IIIb	0	WL_{max}, $Days_{flooded}$	From R	30	−92.02	0.18

Note. Model III AIC values are not directly comparable to Models I and II. AIC = Akaike's information criteria.

information criterion (AIC; Akaike, 1974). AIC is a statistical criterion that balances goodness of fit with model parsimony by rewarding goodness of fit but including a penalty term based on the number of model parameters. The DFM with the smallest AIC is preferred, and we also used the relative likelihood function to compare different statistical models following Burnham and Anderson (2002):

$$RLi = \exp\left[\frac{AIC_{min} - AIC_i}{2}\right], \qquad (3)$$

where RLi is relative likelihood that a particular model is the "best" (percentage), AIC_{min} is the lowest AIC of all models, and AIC_i is the AIC of a particular model.

Model II was developed by incorporating explanatory variables into the DFA until a combination of common trends and explanatory variables was identified that met or exceeded the goodness-of-fit indicators from Model I (without exceeding the VIF criterion). Model II thus aims to achieve similar model fitness with reduced reliance on latent variation (i.e., with fewer common trends). Model II also aims to reduce $\rho_{m,n}$ and $\gamma_{m,n}$ of any remaining trends, indicating reduced dependency on unknown variation. Further reduced models were then explored by using the explanatory variables identified in Model II to create multilinear models without common trends to assess our ability to model the system based solely as a function of known hydrologic variation. Model IIIa used all explanatory variables from Model II, and Model IIIb used a subset of explanatory variables selected using forward and backward step-wise variable selection with AIC as the selection criteria. Multiple regression and model selection were performed in R (R Core Development Team, 2016). To compare the relative importance of common trends and explanatory variables across response variables (Zuur et al., 2003; Zuur & Pierce, 2004), all series were normalized before analysis (mean subtracted, divided by standard deviation).

3 | RESULTS

3.1 | Response and explanatory variables

Forty-eight species or groups of species were landed by the Z-1 Fishermen's Colony from 1990 to 2007; here, we focus on the 10 most abundant and commercially important species (Figure 2), which represent over 80% of the total recorded landings by mass. Total annual catch averaged over the 18-year period of record was 848.5 t year^{-1}. Species with the highest catch included curimatã, followed by dourada/filhote, and pacu. The highest fish production (894 t) was recorded in 1993, and the lowest catch (271 t) was

observed the following year. Temporal variance in catch was high across all species (Figure 2) but was most pronounced for jatuarana, surubim, and tucunaré.

Observed and derived hydrologic variables are shown in Figure 3. Water level (min, max, and mean) and discharge showed strong and regular wet/dry seasonal patterns with four major phases: rising limb (November, December, and January), maximum flood stage (February, March, and April), falling limb (May, June, and July), and dry season (August, September, and October). Minimum and maximum flows and levels occurred in the dry season of 2005 and the rainy season of 1997, respectively (Figure 3); however, year-to-year variance in flow minima and maxima were relatively small. Seasonal patterns were directly reflected in lagged metrics and increment, whereas the "days flooded" variable had nonzero values for a subset of the wettest years (3, 29, and 73 days in 1991–1993, respectively; 63 days in 1997 and 25 days in 2001).

3.2 | Dynamic factor analysis

3.2.1 | Baseline DFA with no explanatory variables (Model I)

We found that four trends ($M = 4$) were required to adequately describe the variation in landings of the 10 fish species; addition of a fifth trend improved R^2 but increased AIC, indicating over parameterization (Table 3). The four-trend Model I AIC value of 4,097 was used as a target for subsequent DFMs. Table 4 summarizes Model I results for each trend (M) and species (n). Level parameters were all insignificant, as expected given data normalization. Overall goodness of fit for Model I was fair ($R^2 = 0.51$) and highly variable across species ($0.16 \leq R^2 \leq 0.95$). Canonical correlation coefficients ($\rho_{m,n}$) indicate the degree of correlation between fitted common trends and response variables. Though only describing latent (unknown) variability at this stage, the four common trends from Model I and their patterns of correlation with each species (Figure 4) were useful for developing ideas about shared variation in catch among species and identifying potentially useful explanatory variables. For example, Trend 1 was moderately to highly correlated (positively) with curimatã, pacu, sardinha, and surubim. Jatuarana and piau had low correlations with Trend 1, and correlation with the remaining four species were minor. For the remaining three trends, moderate to high correlations existed between Trend 2 with dourada/filhote ($\rho = 0.74$); Trend 3 with jatuarana ($\rho = 0.56$); and Trend 4 with branquinha ($\rho = −0.53$); all other correlations were low or minor. These results were generally mirrored in the Model I factor loading ($\gamma_{1,n}$) values (Table 4).

Although there were a limited number of moderate and high correlations between common trends and response variables, visual
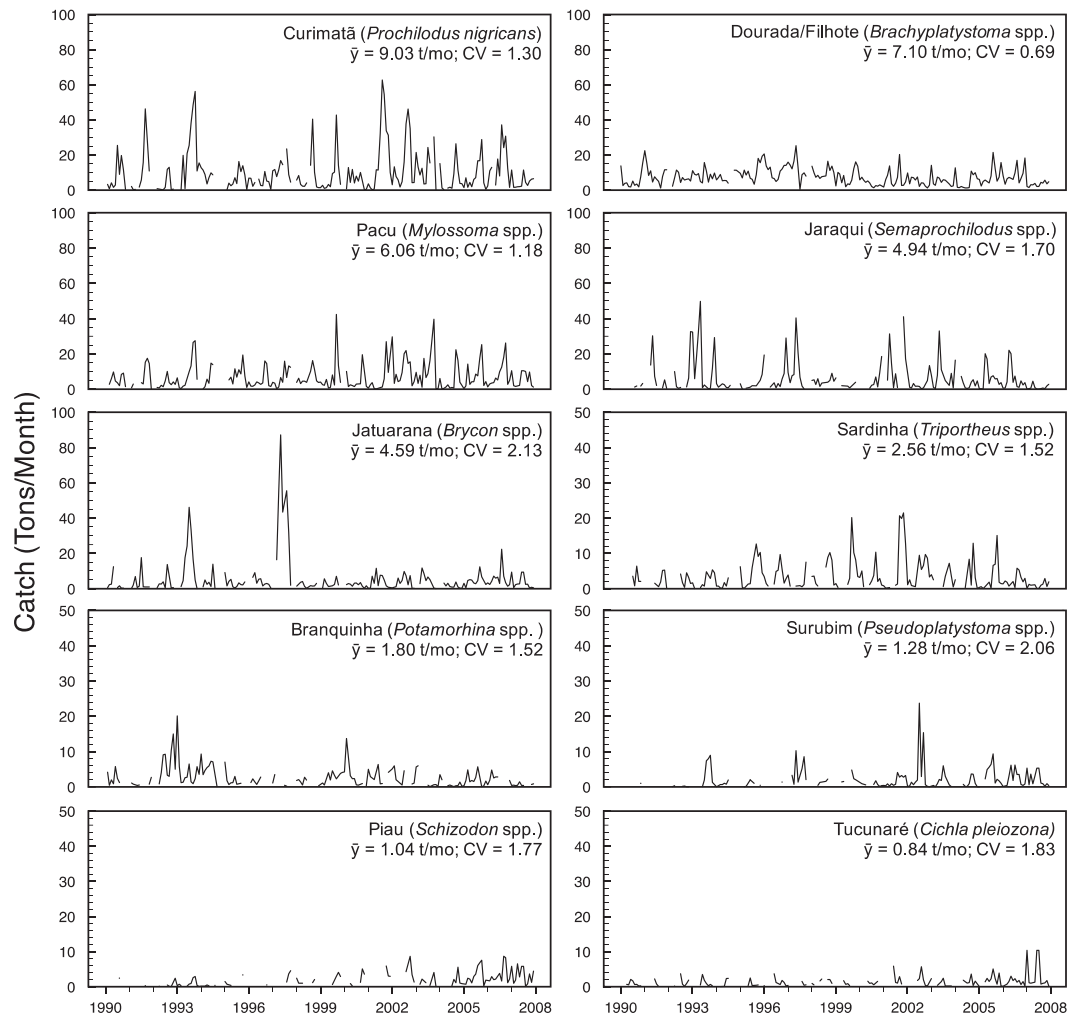
FIGURE 2 Reported fish catch for the 10 main commercial species landed in Porto Velho from 1990 to 2007. Data provided by the Z-1 Fisher Association. Note change in y-axis scale. CV = coefficient of variation

inspection of the four fitted trends provided insight into the processes driving variation for the species that exhibit some degree of correlation. For example, Trend 1 (Figure 4) exhibited strong and regular year-to-year variation representative of the seasonal hydrologic pulsing observed on the Madeira River (Figure 3). Yearly peaks in Trend 1 generally occurred in the dry season, with the highest magnitude seasonal maxima in 1993, 1999, 2001, and 2002. Figure 4 illustrates that the strongest correlations with Trend 1 were for curimatã, pacu, sardinha, surubim, and piau. Trend 2 (Figure 4) showed some high-frequency (year-to-year) variation but also exhibited an apparent lower-frequency oscillation, ascending through the early 1990s, declining consistently in the late 1990s, and again increasing after 2000. Strongest correlations with Trend 2 were for dourada/filhote, jaraqui, and jatuarana (Figure 4). Trend 3 was characterized by noise around zero with two distinct peaks in 1992 and 1997 (Figure 4), 2 years with the highest recorded water levels and a large number of flooded days (Figure 3); this trend was most strongly correlated with jaraqui, jatuarana, and branquinha (positive) and piau (negative; Figure 4). Finally, Trend 4 showed longer-scale variation from strongly negative to strongly positive (Figure 4) and had variable (and low) correlation with all species except branquinha (Figure 4).

Model I fits to observed data are illustrated in Figure 5 and were fair to excellent ($0.52 \leq R^2 \leq 0.95$; Table 4) for six of 10 species. Model I did a good job of capturing peaks in production across different years in the period of record for most species (e.g., curimatã, pacu, dourada/filhote, jatuarana, sardinha, and surubim) but missed these variations in branquinha and tucunaré. Notably, the four species with poorer fits ($0.16 \leq R^2 \leq 0.40$) were relatively data scarce, with the exception of jaraqui (Table 4), highlighting the role of data completeness in trend fitting. This is evidenced by both low $\rho_{m,n}$ and $\gamma_{m,n}$ values and model performance for these species (see Section 4).

3.2.2 | DFA with explanatory variables (Model II)

As expected, VIFs among some hydrologic variables (e.g., minimum, average, and maximum water level) were high, and only combinations of variables that met the VIF < 5 criteria were used. This resulted in 98 different DFMs using combinations of the 11 candidate explanatory variables and varying numbers of common trends. We found the best DFM used four explanatory variables ($K = 4$; $1.05 \leq$ VIF ≤ 4.41): WL_{max}, $Days_{flooded}$, Q_{y-1}, and increment. Using these explanatory variables allowed us to reduce the number of required common trends
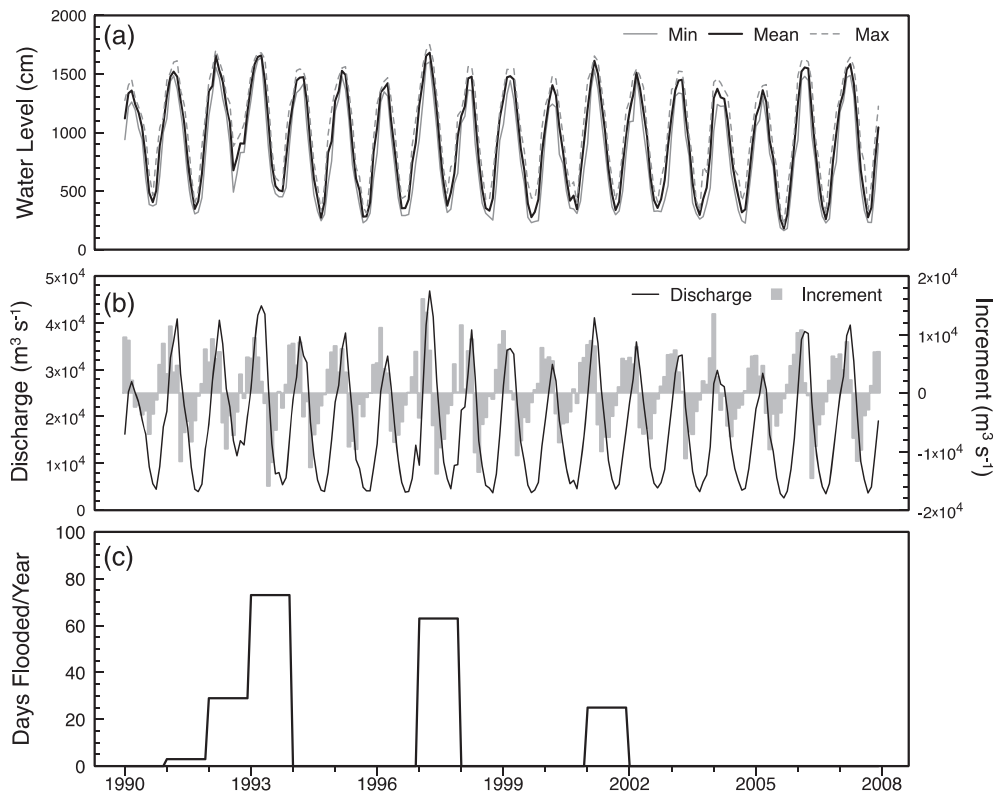
FIGURE 3 (a) Minimum, average, and maximum monthly water level in centimetres (cm) above mean sea level measured at Porto Velho, (b) mean monthly discharge and increment (change in discharge) measured at the same station, and (c) number of days water level exceeded 1,600 metre above sea level cm, a threshold identified as important to fisheries production by member of the Z-1 Fisher Association. Water level and discharge data from the Mineral Resources Research Company

TABLE 3 Akaike's information criteria (AIC), R-squared and relative likelihood values for dynamic factor models with no explanatory variables (i.e., Model I) and 1–5 common trends (M)

M	R^2	AIC	Relative likelihood (%)
1	0.25	4283	0
2	0.40	4169	0
3	0.46	4119	0
4	**0.54**	**4097**	**N/A**
5	0.56	4101	14

Note. Best model is rendered in bold.

to one ($M = 1$), reducing unexplained variability in the model while achieving similar performance as Model I. The selected Model II had an AIC of 4,054, lower than the 4,098 from Model I (Table 2), and the lowest of any DFM built using available explanatory variables (see Supporting Information for full Model II results).

Table 5 summarizes Model II results. Level parameters were again all insignificant due to data normalization. Despite having a reduced AIC value, Model II fitness as measured with R^2 was lower than for Model I (overall $R^2 = 0.38$; $0.14 \leq R^2 \leq 0.71$). Values of $\rho_{m,n}$ and $\gamma_{m,n}$ for the one trend remaining in Model II were reduced relative to Model I, indicating less reliance on latent variation, but were still

TABLE 4 Proportion of months with data (% data), constant level parameters (μ_n), canonical correlation coefficients ($\rho_{m,n}$), factor loadings ($\gamma_{m,n}$), and coefficients of determination (R^2) for each species in Model I

| Species	% Data	μ_n	$\rho_{1,n}$	$\rho_{2,n}$	$\rho_{3,n}$	$\rho_{4,n}$	$\gamma_{1,n}$	$\gamma_{2,n}$	$\gamma_{3,n}$	$\gamma_{4,n}$	R^2
Curimatã	87	−0.03	0.88	−0.02	0.19	−0.21	0.56	−0.05	0.15	−0.02	0.77
Dourada/Filhote	96	0.00	0.05	0.74	−0.06	0.09	0.04	0.31	0.12	−0.02	0.55
Pacu	87	−0.02	0.71	−0.07	−0.08	0.00	0.51	−0.05	0.04	0.03	0.56
Jaraqui	75	0.01	−0.01	0.30	0.28	−0.23	−0.08	0.12	0.08	−0.07	0.18
Jatuarana	80	−0.01	0.31	0.48	0.56	0.17	0.04	0.02	0.56	0.00	0.95
Sardinha	72	−0.12	0.64	0.17	−0.28	−0.09	0.53	0.12	−0.12	0.01	0.71
Branquinha	68	−0.03	0.02	0.09	0.38	−0.53	−0.05	0.07	−0.08	−0.12	0.31
Surubim	57	−0.17	0.52	−0.01	0.09	0.16	0.32	−0.13	0.19	0.05	0.40
Piau	45	−0.20	0.41	−0.12	−0.42	0.40	0.38	−0.09	−0.02	0.11	0.52
Tucunaré	55	−0.09	0.06	−0.24	−0.05	0.24	0.05	−0.14	0.10	0.07	0.16
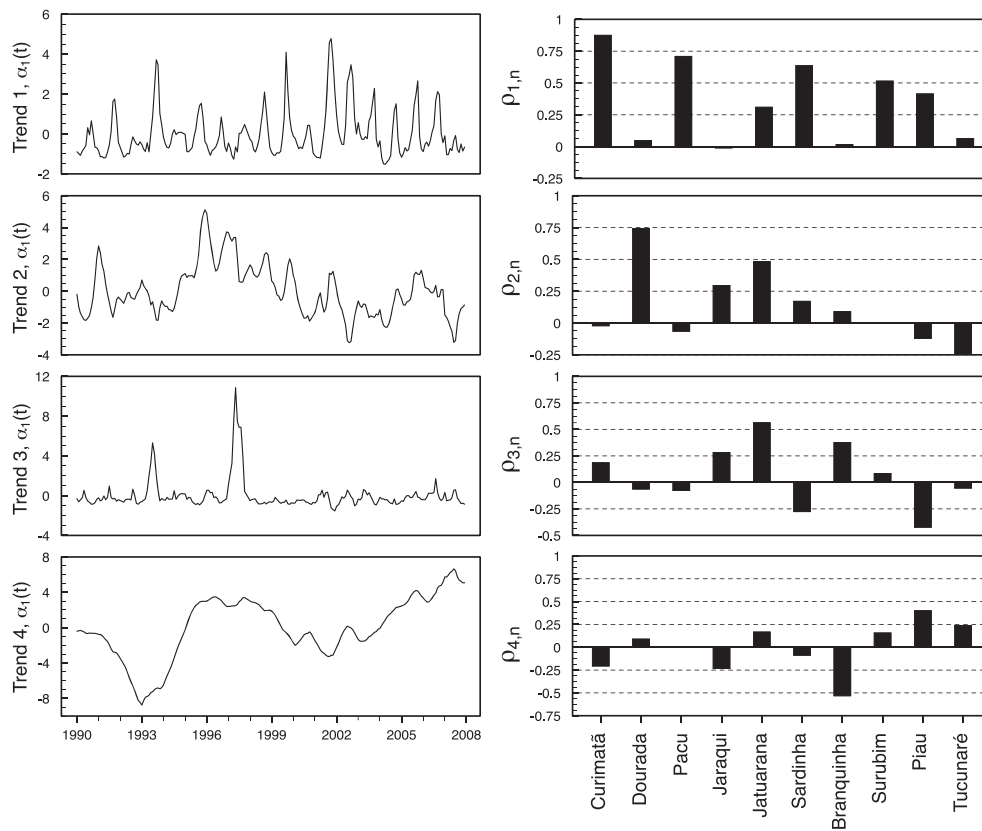
FIGURE 4   The four trends from Model I (left) and their associated canonical correlation coefficients (right)

important for some species. The trend was moderately correlated with jatuarana, piau (positively), and branquinha (negatively); surubim, dourada/filhote, and tucunaré had low correlations, and correlation with the remaining four species were minor. Trend 1 (Figure 6a) does not exhibit regular year-to-year variation (likely accounted for by explanatory variables in Model II), but instead appears to represent distinct low (1992–1993) and high (1997–1998, 2002, and 2005–2006) catch periods that are not represented by explanatory variables.

The importance of each explanatory variable to each fish species is given by the magnitude and significance of regression coefficients ($\beta_{k,n}$). Maximum water level (WL_{max}) had the highest $|\beta_{k,n}|$ values and was a significant predictor for seven of 10 species (Table 5 and Figure 6). Negative $\beta_{k,n}$ values are explained by cross-correlation patterns in hydrologic variables and species life histories (presented below). Values of $\beta_{k,n}$ for previous year's flow (Q_{y-1}) were only significant for curimatã and pacu (positive), and jaraqui (negative), whereas correlation with days flooded was relatively high, positive, and significant for a subset of species: curimatã, dourada, jaraqui, and jatuarana (Figure 6). Values of $\beta_{k,n}$ for increment were significant for five species, had variable sign, and were generally low. All species had a significant relationship with at least one explanatory variable, with the exception of piau.

Model II fits to observed data are illustrated in Figure 7. Model fits were lower than those from Model I (Figure 5), but still captured coarse patterns of intra-annual and interannual variation for most species. In general, Model II was best at predicting repeating year-to-year catch variation (e.g., for curimatã, pacu, sardinha, and surubim) and distinct extreme catch years (e.g., for jatuarana). Species with "noisier" temporal variation (dourada, jaraqui, branquinha, and piau) were less well

predicted. As with Model I, the poorest fit was for tucunaré ($R^2 = 0.16$), which had the least available data (55%; Table 4), although this poor fit may also be due to anomalously high catch data from the end of the period of record (Figure 7).

Cross-correlations analysis showed highly variable relationships between lagged hydrologic variables and fish catch for each species. The strongest consistent lagged correlations were for water level lagged by 6 months, flooded days lagged by 2 months, flow lagged by 8 months, and increment lagged by 10 months (Table 6). A DFM using these explanatory variables ($1.09 \leq VIF \leq 3.43$) and one trend had an AIC of 4,076 (i.e., better goodness of fit than Model I, but not as good as the selected Model II) and was thus not explored further. However, CCA results helped to explain the variable sign of $\beta_{k,n}$ seen for some explanatory variables (Figure 6; see Section 4).

3.2.3 | DFA with no common trends (Model III)

Finally, all common trends were removed to assess the predictive power of a DFM using only the explanatory variables identified in Model II (i.e., a multilinear regression model). As expected, R^2 values for Model IIIa and IIIb were reduced from those in Model II (Table 7). With common trends removed, 16 of 40 parameters (40%) were significant to Model IIIa and 12 of 20 (60%) were significant to Model IIIb, compared to 20 of 40 (50%) in Model II, suggesting that process for identifying explanatory variables in Model II is relatively robust. The relative importance of explanatory variables in Model IIIa was similar to that in Model II, with average absolute model parameter values of 0.41, 0.18, 0.23, and 0.15 for WL_{max}, $Days_{flooded}$, Q_{y-1}, and increment,
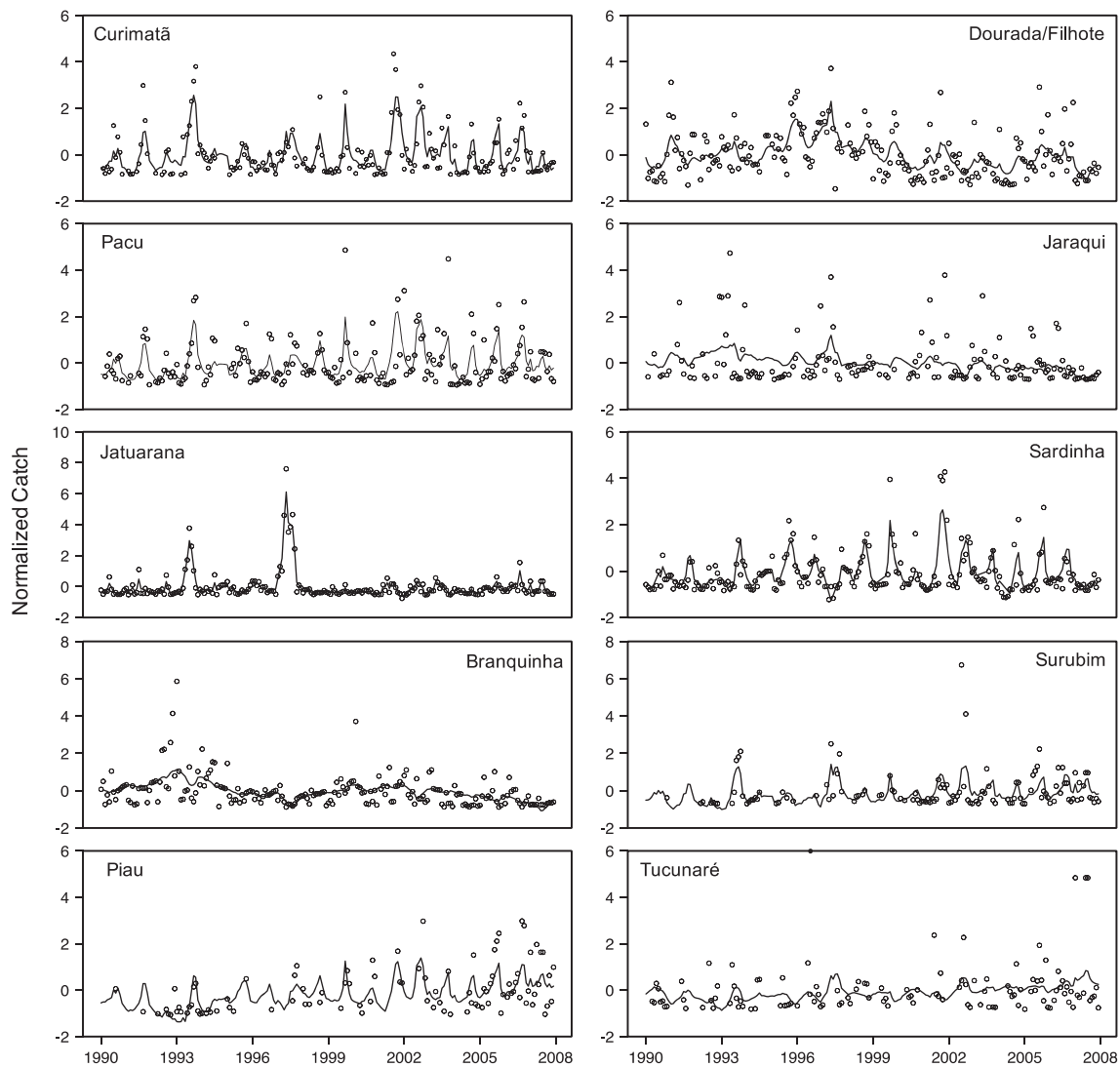
FIGURE 5 Observed (lines) and modelled (open circle) normalized catch for each species in Model I

TABLE 5 Constant level parameters (μ_n), canonical correlation coefficients ($\rho_{m,n}$), factor loadings ($\gamma_{m,n}$), regression coefficients ($\beta_{k,n}$), and coefficients of determination (R^2) for Model II

Species	μ_n	$\rho_{1,n}$	$\gamma_{1,n}$	$\beta(WL_{max})$	$\beta(Days_{flooded})$	$\beta(Q_{y-1})$	$\beta(increment)$	R^2
Curimatã	−0.01	0.05	0.04	**−0.85**	**0.36**	**0.33**	0.07	0.45
Dourada/Filhote	0.01	0.29	0.12	−0.01	**0.22**	−0.06	**0.23**	0.26
Pacu	−0.01	0.13	0.05	**−0.78**	0.12	**0.25**	0.05	0.44
Jaraqui	0.00	−0.08	−0.02	**0.63**	**0.26**	**−0.43**	−0.07	0.27
Jatuarana	−0.03	0.50	0.24	−0.06	**0.64**	0.14	**−0.21**	0.71
Sardinha	−0.13	0.03	0.00	**−0.72**	0.08	0.08	**0.27**	0.40
Branquinha	−0.09	−0.53	−0.20	**0.33**	0.07	−0.21	0.00	0.33
Surubim	−0.09	0.35	0.14	**−0.36**	0.17	0.14	**−0.19**	0.43
Piau	−0.07	0.52	0.20	−0.12	0.02	−0.18	0.11	0.38
Tucunaré	−0.13	0.22	0.11	**0.28**	−0.07	−0.22	**−0.38**	0.14

Note. Significant β are shown in bold.

respectively (compared to 0.41, 0.20, 0.20, and 0.16 for Model II). For the more reduced Model IIIb, the relative importance of explanatory variables was shared equally between the remaining variables (average absolute parameter values of 0.26 and 0.23 for WL_{max} and $Days_{flooded}$, respectively).

4 | DISCUSSION

This study is the first to present a quantitative measure of fisheries production in the Madeira River fishery, detailing 18 years of monthly fish catch data for the 10 most commercially important species
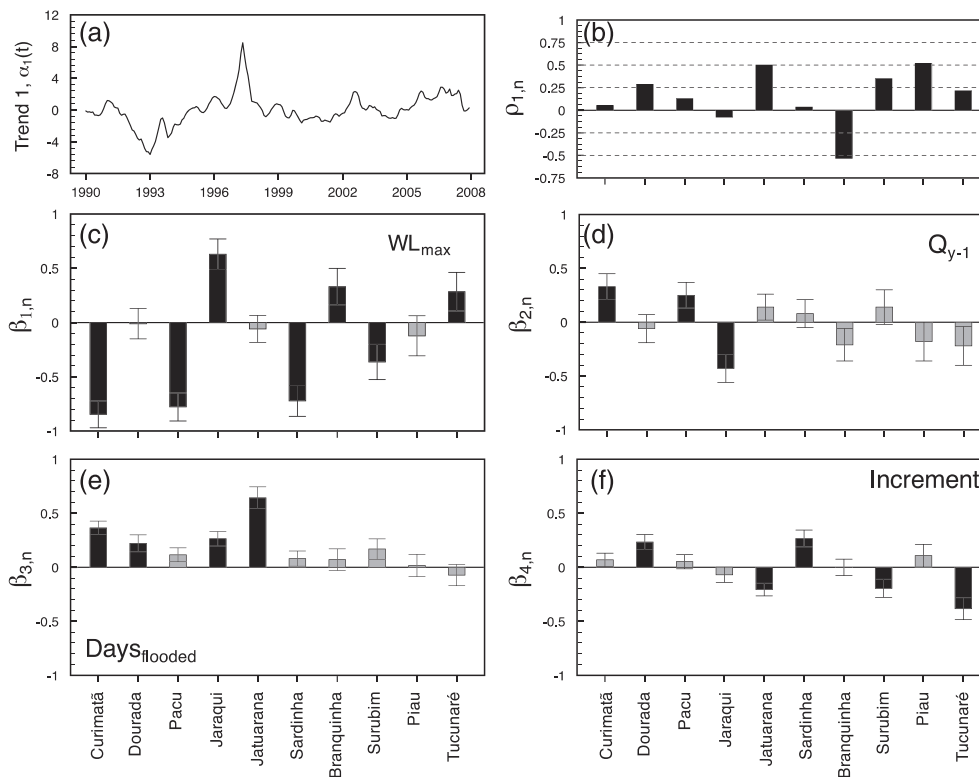
FIGURE 6 The (a) common trend, (b) canonical correlation coefficients, and (c–f) regression coefficients for each explanatory variable from Model II ($M = 1$, $K = 4$)

landed at the region's largest market. Analysing these data using dynamic analysis (DFA) allowed us to (a) develop models that evaluate which hydrologic variables were most important in explaining catch for each species; (b) provide a baseline for understanding how fish catch is likely to change in the dammed system; and (c) develop preliminary recommendations for dam management to mitigate these changes.

4.1 | The Madeira River fishery and the role of fishermen

The Madeira River fishery is thought to currently support approximately 2,000 fishermen (Doria et al., 2015) in the state of Rondônia, although the "official" count of fishermen is dynamic. Around 70 fish species are used in the region's artisanal commercial fisheries, and the mean fish consumption is around 500 g per capita per day (Doria et al., 2015). Among the 10 most commercially important species analysed here, average monthly catch varied by an order of magnitude among species (i.e., from 0.84 t month^{-1} for tucunaré to 9.03 t month^{-1} for curimatã; Figure 2). Some species were characterized by a clear annual production cycle (e.g., curimatã, pacu, jaraqui, and sardinha), and others were landed more consistently throughout the year (e.g., dourada/filhote) or had noisy and sporadic catch patterns (e.g., jatuarana, branquinha, surubim, piau, and tucunaré). Overall, catch data also reinforce the importance of medium- and long-distance migratory species such as curimatã, dourada/filhote, and pacu for total fisheries production in the Madeira River. These three migratory species accounted for 57% of total catch by mass, emphasizing the

importance of understanding the factors that connect reproduction and trophic dispersion with variations in the water cycle.

Fishermen clearly play a strong role in driving variation in fish catch, and information about fisheries effort (in addition to overall fish catch) is therefore fundamental to assessing fisheries production and diversity (Castello et al., 2015). Fishing effort data are scarce in many regions (including the Madeira), however, and fish catch data are often the only data available (Carruthers et al., 2014), especially for small-scale fisheries. In general, a lack of fish catch and fishing effort data across the Amazon makes it difficult to assess health of the fishery and threatens the management and conservation of fish stocks (Ruffino, 2014). This limitation is related to the size of the region and other attributes of the fishery, such as the large number of workers fishing over vast areas, a high diversity of species, gear and techniques, and the locations of landings in diffuse or in isolated area (Barthem & Fabré, 2004; Castello, Viana, Watkins, Pinedo-Vasquez, & Luzadis, 2009).

Despite lacking estimates of effort, these data serve as a baseline for understanding potential changes to the fishery resulting from the recent construction of the Santo Antônio and Jirau dams and provide support for the idea that long-term monitoring is a key for maintaining a sustainable fishery in the face of change. Beyond Brazil, fisheries in Bolivia and Peru, which make up nearly 60% of the overall Madeira basin area, are also vulnerable to changes in fisheries production from dam construction both within and outside of their borders (Finer & Jenkins, 2012), particularly in relation to high-value migratory species such as dourada. For example, interruption of long-distance migratory routes has the potential to impact as many as 3,000 Bolivian fishermen (MMAyA, 2014).
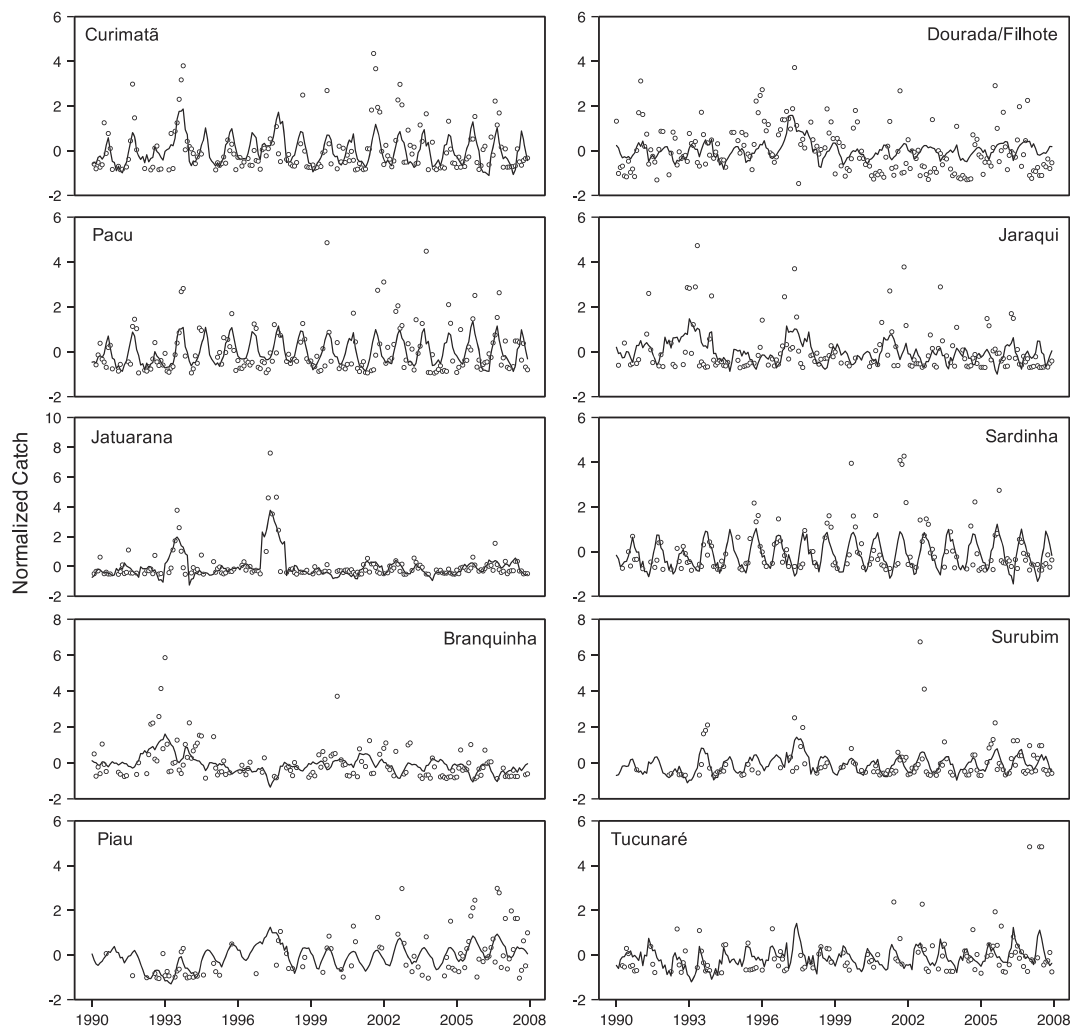
FIGURE 7 Observed (lines) and modelled (open circle) normalized catch for each species in Model II

TABLE 6 Pearson correlation values between response variables and four lagged explanatory variables (m−2: two previous months; m−6: six previous months; m−8: eight previous months and m−10: ten previous months)

Species	$WL_{min,m-6}$	$Days_{flooded,m-2}$	Q_{m-8}	$Increment_{m-10}$
Curimatã	0.54	0.25	0.21	0.23
Dourada/Filhote	−0.01	0.14	0.21	0.22
Pacu	0.53	0.03	0.22	0.27
Jaraqui	−0.15	0.32	0.08	0.04
Jatuarana	0.05	0.53	−0.18	−0.14
Sardinha	0.45	−0.03	0.32	0.33
Branquinha	0.02	0.22	0.12	0.07
Surubim	0.29	0.14	−0.09	0.02
Piau	0.25	−0.23	0.13	0.19
Tucunaré	−0.09	−0.09	−0.21	−0.14

4.2 | Model I—Interpreting common trends

Analysis of canonical correlation coefficients ($\rho_{m,n}$) between common trends and fish catch in Model I revealed patterns of shared variance among species (Figure 4) based on life history strategy. Species with similar migration patterns can be clustered into groups according to

their $\rho_{m,n}$. For example, three species in the order characiformes (curimatã, pacu, and sardinha) and one in the order siluriformes (surubim), all of which undertake medium-distance migration, had moderate to high (positive) correlations with Trend 1. These species have a strong adaptation to cyclic annual precipitation and flow regimes, with dry seasons and floods triggering trophic and reproductive migrations (Ruffino & Isaac, 1995). Specifically, the flood period is characterized by migratory behaviour and reproduction of many species, which use flooded areas for the deposit and dispersal of eggs and larvae. During maximum flood stage, these fish are widely dispersed in flooded habitats and fisheries catch decreases (Barthem & Fabré, 2004; Halls & Welcomme, 2004). As waters recede, adult fish return to the river channel and become easier to catch, especially for shoaling species (Barthem & Goulding, 1997; Ribeiro & Petrere, 1990). Fishermen increase their fishing effort to take advantage of the vulnerability of these species, which are concentrated in smaller environments during the dry season (Mérona & Gascuel, 1993). This temporal pattern was well characterized by the yearly dry season peaks in Trend 1, helping to explain trend correlation structure for these species.

For Trend 2, only the long-distance migratory species dourada (order Siluriforms) was highly correlated. Dourada are able to migrate approximately 4,000 km from the mouth of the Amazon estuary to

TABLE 7 Regression coefficients ($\beta_{k,n}$) and coefficients of determination (R^2) for Models IIIa and IIIb

	Model IIIa						Model IIIb			
	Int.	$\beta(WL_{max})$	$\beta(Days_{flooded})$	$\beta(Q_{y-1})$	$\beta(Increment)$	R^2	Int.	$\beta(WL_{max})$	$\beta(Days_{flooded})$	R^2
Curimatã	−0.01	**−0.83**	**0.36**	**0.31**	0.07	0.37	0.00	**−0.52**	**0.33**	0.35
Dourada/Filhote	0.01	0.03	**0.19**	−0.12	**0.23**	0.09	0.00	0.00	**0.17**	0.03
Pacu	−0.01	**−0.76**	0.10	0.23	0.05	0.30	−0.01	**−0.54**	0.08	0.29
Jaraqui	−0.01	**0.60**	**0.27**	**−0.40**	−0.06	0.22	−0.01	**0.23**	**0.29**	0.18
Jatuarana	0.00	0.07	**0.59**	−0.02	**−0.19**	0.36	0.03	0.00	**0.61**	0.33
Sardinha	−0.13	**−0.72**	0.08	0.08	**0.27**	0.32	−0.09	**−0.53**	0.03	0.27
Branquinha	−0.02	0.32	**0.22**	−0.17	0.00	0.09	−0.03	0.17	**0.23**	0.08
Surubim	−0.06	−0.30	0.17	0.07	**−0.21**	0.15	−0.03	**−0.28**	**0.19**	0.11
Piau	−0.08	−0.18	−0.16	−0.18	0.04	0.16	−0.08	**−0.32**	−0.32	0.15
Tucunaré	−0.13	0.28	−0.13	−0.25	**−0.37**	0.11	0.01	0.04	−0.09	0.01

Note. Significant β are shown in bold.

the headwaters of Andean rivers in Ecuador, Peru, Colombia, and Bolivia to spawn (Cella-Ribeiro et al., 2015; Duponchelle et al., 2016; García Vásquez et al., 2009). Like Trend 1, Trend 2 exhibits annual variation but is usually out of phase with Trend 1, with peaks during the rising limb of the hydrograph. This may be explained by the migration of species such as dourada during the rising limb, when they are restricted to the river channel and thus vulnerable to fishing (García Vásquez et al., 2009). As noted above, Trend 2 also had lower-frequency variation with three distinct periods corresponding to oscillation between low and high periods: 1990–1994 (below average); 1994–2000 (above average); and 2000–2007 (below average). It is not clear what is driving this longer temporal scale variation; correlations between Trend 2 and standard climate indices (e.g., Atlantic Multi-decadal Oscillation, Pacific Decadal Oscillation, Sea-surface temperature anomalies, and various El Niño–Southern Oscillation [ENSO] indices) were all insignificant. However, the flood pulse in the Amazon is influenced by rainfall in the drainage basin associated with the Andean thaw, and the spatial and temporal variations are intensified by ENSO effects that cause accentuated droughts and floods (Pielke & Landsea, 1999). Longer-scale temporal variations may also reflect biotic interactions that modify the structure of local fish communities. For example, in low-water periods, there is increased predation and therefore possible effect on the recruitment of fisheries in subsequent years (Sousa & Freitas, 2008; Vieira, Garcia, & Grimm, 2008).

Trend 3 largely represented peaks in fish catch in the high flood years of 1993 and 1997. There were significant correlations between Trend 3 and some climate indices (ENSO and Pacific Decadal Oscillation); however, this trend was better characterized by the number of days flooded (see Section 4.3). The duration and intensity of hydrologic fluctuations may facilitate or undermine the recruitment success of different species (Bittencourt & Amadio, 2007). Environments with longer periods of intense floods provide protection and reduce the vulnerability of fish larvae to natural predation, thus favouring the recruitment of individuals to the environment (Vieira et al., 2008). Jatuarana, a medium-distance migratory species of the order Characiforms, had the highest correlation with Trend 3 ($\rho_{3,5}$ = 0.56), followed by branquinha and jaraqui. Visual inspection of Figure 2 reveals distinct peaks in catch for these species in 1993 and

1997 (except for branquinha in 1997, when data were missing). Jatuarana just missed the moderate correlation cut-off with Trend 2, with $\rho_{2,5}$ = 0.48, but the model for this species has the highest overall correlation with all trends (i.e., maximum $\rho_{m,n}$), indicating that the Model I DFM for this species relied on shared variation among all four trends. Finally, Trend 4 had moderate (negative) correlation with branquinha and low (positive) correlation with piau. Given the shape of Trend 4, this may be interpreted as an oscillating but generally decreasing trend in the catch of branquinha ($\rho_{4,7}$ = −0.53) and a gradually increasing trend in the catch of piau ($\rho_{4,9}$ = 0.40) since 1993. This is supported by the raw fish catch data, which show a negative trend in branquinha catch ($p <$ .001) and a positive trend in piau catch ($p <$ .001) from 1993 through 2008 (not shown). Although the mechanism(s) for these patterns remain unknown, Trend 4 was useful in identifying these general trends, which were not apparent from visual inspection of the raw data (Figure 2).

4.3 | Models II and III—Interpreting explanatory variables

Development of Model II allowed us to identify the set of explanatory variables that best described variation in fish catch across all 10 species. These results are important because they use relatively simple and widely observed hydrologic data to predict fish catch in the natural (i.e., undammed) system. This approach yielded one distinct best Model II that used four (sufficiently independent) hydrologic variables and one common trend. We also applied these variables to develop multilinear models with no trends (Models IIIa and IIIb). Models II and IIIa and IIIb revealed similar patterns in the relative magnitude and sign of correlations ($\beta_{k,n}$) between observed fish catch and each variable. Because all response and explanatory variables were normalized before analysis, the relative magnitude of these $\beta_{k,n}$ values can be interpreted as weights, with higher values having more importance in the resulting model. Values of $\beta_{k,n}$ from Models II and IIIa were similar; for simplicity, we refer to those from Model II in the discussion below. Fitted $\beta_{k,n}$ indicate that, in general, WL_{max} was the strongest driver of overall variation in observed fish catch (mean $|\beta_{k,n}|$ = 0.41), whereas $Days_{flooded}$, Q_{y-1}, and increment were all

about half as important (mean $|\beta_{k,n}|$ = 0.20, 0.20, and 0.16, respectively). Critically, however, this ordering of importance is not consistent across species. For example, days flooded provided the strongest explanation for variation in catch of jatuarana ($\beta_{3,5}$ = 0.59), whereas WL_{max} was insignificant for this species (Table 7). Similarly, increment was the best predictor for tucunaré ($\beta_{4,10}$ = −0.37) and was this species' only significant explanatory variable.

Figure 6 summarizes the magnitude, sign, and significance of the correlation between each response and explanatory variable, illustrating the unique relationship between each fish species and the hydrological variables in Model II. The strong seasonal cycling of WL_{max} served to replace (in part) the temporal variation previously provided by Trend 1 in Model I, and we invoke the same general mechanistic connection to explain these correlations (i.e., trophic and reproductive migrations triggered by cyclic flow regimes), which were significant for seven of 10 species. Strong negative $\beta_{k,n}$ values for curimatã, pacu, sardinha, and surubim are explained by the CCA (Table 6). In short, when water levels are high, catch for these species is low, and vice versa. This relationship shows up as a negative unlagged correlation or a positive correlation if lagged by 6 months because of the region's cyclical high-low water cycle (Figure 3), which exhibits strongest negative autocorrelation at lags of 6 months. Thus, the high lagged correlations in Table 6 correspond to the negative $\beta_{k,n}$ found between WL_{max} and catch of curimatã, pacu, sardinha, surubim, and piau (Figure 6).

Values of $\beta_{k,n}$ for Q_{y-1} and $Days_{flooded}$ were all positive (except for piau), moderate in magnitude, and significant for the same four species (Figure 6). The sign of this relationship is consonant with the concept that high flow years, particularly those with flood stages above a critical level for floodplain connection, are associated with increased productivity (Castello et al., 2015; Junk et al., 1989). Differences in the exact timing of the flood cycle from year to year reduced correlation among Q_{y-1} and other water level/flow variables sufficiently for its use in Model II (i.e., its addition did not increase VIF > 5); however, it exhibited a similar cyclic pattern. As such, in Model II, Q_{y-1} was associated with species with peaks in catch that are out of phase with WL_{max}. In this sense, Q_{y-1} (in part) took the place of Trend 2 in Model I. Strong similarities between the $Days_{flooded}$ variable and Model I Trend 3 further support the idea of "trading" unknown for explained variation. Trend 3 from Model I mirrored the $Days_{flooded}$ peaks in 1993 and 1997, though it missed the shorter 2001 flooding event. Similar to $\rho_{3,n}$ values from Model I, $\beta_{3,n}$ values for Model II were highest for jatuarana, and strong reliance on this variable is reflected in the model fitted to these data (Figure 7).

Values of $\beta_{k,n}$ for increment were significant for five species, but they were lowest in magnitude and variable in sign. No obvious relationship between this explanatory variable and Trend 4 from Model I was apparent, either in temporal variation or the magnitude/sign of associations. The time lag between reproduction and eventual harvest (and variation in this lag among species) likely make this explanatory variable less effective in predicting fish catch. Across variables, interpretation of the interactions among explanatory variables and observed fish catch by species allows us to make preliminary conclusions about the role of flow in structuring fisheries dynamics and provides guidance for future dam operation (discussed below). The most reduced model (Model IIIb) achieved global model parsimony

(i.e., minimum AIC) by dropping increment and Q_{y-1} as explanatory variables (Table 2). As a result, Model IIIb had reduced predicative ability, particularly for the species for which increment was a significant predictor (dourada, jaraqui, sardinha, and tucunaré; tucunaré Table 7).

Challenges in selecting the best set of explanatory variables include balancing model fitness versus number of parameters (i.e., model parsimony), avoiding multicollinearity, and interpreting model results relative to species-specific biological and ecological knowledge. Although AIC is widely used to overcome the first challenge, in systems with several colinear variables, selection of the best set of explanatory variables (and maintain VIF below threshold selected a priori) becomes more arbitrary. For example, our best Model II used four explanatory variables (WL_{max}, $Days_{flooded}$, Q_{y-1}, and increment) and one common trend, with an AIC value of 4,054. Two models with similar fitness, one using only three explanatory variables (WL_{max}, $Days_{flooded}$, and increment) and one using five explanatory variables (WL_{max}, $Days_{flooded}$, $Days_{flooded,y-1}$, Q_{y-1}, and increment) had AIC values of 4,062 and 4,061, respectively (see Supporting Information). The relative likelihood approach (Equation 3) indicated low probabilities (<2%) that these models were best, but the three-variable model is compelling for two reasons: (a) it was more parsimonious; and (b) it had a lower VIF (1.03) because water level and lagged flow are inherently correlated given the river's cyclic annual hydrologic cycle (although not enough to exceed the VIF < 5 threshold). Considering predicative ability, the reduced complexity, three-variable model had lower goodness of fit (R^2 = 0.36), but the effect was small (i.e., Model II R^2 = 0.38), suggesting that the AIC parameter penalty may not be strong enough to avoid overfitting relative to small increases in model fitness. Finally, the lack of effort data in this study likely contributes to the poorer fits achieved for some species (Cooke et al., 2016; Inomata & Freitas, 2015; Lorenzen et al., 2016).

4.4 | Planning for and mitigating the impact of dams

Changes in the Amazon's freshwater ecosystems from the development of hydropower will have a cascade of physical, ecological, and social effects at local to global scales (Ferreira et al., 2014; Finer & Jenkins, 2012; Laurance et al., 2001; Winemiller et al., 2016). Dams alter the natural flow regime by changing the magnitude, frequency, duration, timing, and rate of change of flow (Richter et al., 1996) and by modifying the transport of riverine sediments, nutrients, and biota (Ligon, Dietrich, & Trush, 1995), often with negative ecological consequences (Bunn & Arthington, 2002; McCully, 1996; Van Looy, Tormos, & Souchon, 2014). In the case of fisheries, some of these linked social and environmental impacts of dam development may be irreversible. For example, projected species extinctions and reductions in fishing yield (Acreman et al., 2014; Winemiller et al., 2016) threaten to reduce regional income and undermine food security (Castello et al., 2015), particularly for communities that rely heavily on natural resources (Tundisi, 2008).

Reducing the environmental impacts of dams requires the optimization of dam operations to reduce hydrologic regime alterations while also improving our understanding of the links between altered hydrology and impacts to ecological and social systems. These approaches are generally referred to as "environmental

flows," and >200 methodologies to address environmental degradation from flow regulation have been developed (Arthington, Bunn, Poff, & Naiman, 2006). Critically, application of environmental flows methods requires integrative analyses to understand the drivers of hydrological alteration and ecological impacts in aquatic systems in periods before dam implementation (Castello & Macedo, 2015). These studies then serve as a baseline from which to isolate anthropogenic impacts from natural variability (Scarcella et al., 2015) and to derive post-dam conservation and mitigation strategies. This type of analysis is difficult in areas where there is shortage of continuous data, hindering communities and governments in these regions from taking appropriate and sustainable decisions (Escobar, 2015).

In the case of the Madeira River presented here, we found DFA to be a useful statistical time series modelling approach for evaluating trends and their interactions with explanatory variables in the predam setting. Despite lacking the effort data required to estimate abundance (i.e., using catch per unit effort), the production data that were available supported the important role of hydrologic variables in structuring capture patterns (Carruthers et al., 2014; Erzini, 2005). The most important explanatory variable in our model was maximum water level followed by days flooded, river flow of the previous year, and increment, although as noted above, the relative importance of these drivers varied by species. One direct ramification of this finding is that multiple hydrological variables must be considered when predicting the likely effects of flow alterations on a multispecies fishery. Moreover, the unique set of responses to hydrological variations across the 10 species in our study suggests that, in the future, dam operating rules need to closely mimic the natural hydrologic regime (rather than a one-size-fits-all prescribed minimal flow) in order to maintain the biological dynamics of these ecosystems. In particular, high flows (characterized by WL_{max} and $Days_{flooded}$) associated with increased catch the following year are important to maintain, but may be difficult to achieve in the context of reservoir regulation and energy production goals.

Although tying fish production to hydrologic variables was a major goal of this research, another important finding of this study is that hydrologic variation, on its own (i.e., Model IIIa), was only able to explain between 9% and 37% of the observed variance in fish catch (Table 7). As noted above, inclusion of fishing effort would likely improve this prediction; however, defining ecohydrological relationships for the purpose of defining ecologically acceptable flow regimes has proved difficult and ambiguous in many regions due to the complexity of natural systems and the highly site and species-specific literature available (Black, Rowan, Duck, Bragg, & Clelland, 2005; Yang, Cai, & Herricks, 2008). Given this challenge, many authors have concluded that the best approach to maintaining or restoring the ecology of a regulated river is to approximate the full range of natural flow variability (Olden & Poff, 2003; Poff et al., 1997; Richter et al., 1996; Sparks, 1995), with the expectation that hydrology is the primary driver controlling abiotic and biotic riverine processes (Jowett, 1997; Mathews & Richter, 2007; Orth, 1987). This approach was used in recent work to understand how dams have altered hydrologic regime across the Amazon (Timpe & Kaplan, 2017) and can be useful for guiding dam operation schemes in both data-rich and data-scarce basins.

In closing, we note that maintaining the natural characteristics of river flows brings numerous direct and indirect benefits to those who depend on aquatic ecosystems (Acreman et al., 2014). Unfortunately, despite a long history of hydropower development in the Amazon, the cumulative, long-term effects of dams on fish and fisheries remain understudied and undervalued in environmental planning and decision-making in Brazil, both for new and existing dams (de Sousa Júnior & Reid, 2010; Soito & Freitas, 2011). Although Brazil has well-defined environmental impact assessment and mitigation programs (Andrade & dos Santos, 2015), these efforts often fail to apply rigorous and independent science (Fearnside, 2013, 2014), integrate data and knowledge across disciplines (Prado et al., 2016; Soares, 2012), or monitor impacts long enough to guide improved management and possible dam reoperation. These failures of science, policy, and management have had widespread environmental, economic, and social consequences (Ansar, Flyvbjerg, Budzier, & Lunn, 2014; Fearnside, 2016; Lees et al., 2016), highlighting an urgent need to further advance interdisciplinary study of the impacts of dams on coupled social–ecological systems, improve management practices, and support sustainable livelihoods.

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