







RESEARCH ARTICLE

Fisheries management influences phytoplankton biomass of Amazonian floodplain lakes

João Vitor Campos-Silva^{1,2,3,4}  | Carlos A. Peres^{4,5,6}  |
João Henrique Fernandes Amaral⁷  | Hugo Sarmento⁸  | Bruce Forsberg⁹  |
Carlos Roberto Fonseca¹ 

¹Departamento de Ecologia, Universidade Federal do Rio Grande do Norte, Natal, Brazil; ²Institute of Biological and Health Sciences, Federal University of Alagoas, Maceió, Brazil; ³Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, Ås, Norway; ⁴Instituto Juruá, Manaus, Brazil; ⁵School of Environmental Sciences, University of East Anglia, Norwich Research Park, Norwich, UK; ⁶Departamento de Sistemática e Ecologia, Universidade Federal da Paraíba, João Pessoa, Brazil; ⁷Laboratory of Aquatic Ecosystems, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil; ⁸Laboratory of Microbial Processes and Biodiversity, Departamento de Hidrobiologia, Universidade Federal de São Carlos, São Carlos, Brazil and ⁹Vermont Department of Environmental Conservation, Watershed Management Division, Montpelier, VT, USA

Correspondence

João Vitor Campos-Silva
Email: jvpiedade@gmail.com

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Abstract

1. Tropical floodplains secure the protein supply of millions of people, but only sound management can ensure the long-term continuity of such ecosystem services. Overfishing is a widespread threat to multitrophic systems, but how it affects ecosystem functioning is poorly understood, particularly in tropical freshwater food webs. Models based on temperate lakes frequently assume that primary producers are mostly bottom-up controlled by nutrient and light limitations, with negligible effects of top-down forces. Yet this assumption remains untested in complex tropical freshwater systems experiencing marked spatiotemporal variation.
2. We use consolidated community-based fisheries management practices and spatial zoning to test the relative importance of bottom-up versus top-down drivers of phytoplankton biomass, controlling for the influence of local to landscape heterogeneity. Our study focuses on 58 large Amazonian floodplain lakes under different management regimes that resulted in a gradient of apex-predator abundance. These lakes, distributed along ~600 km of a major tributary of the Amazon River, varied widely in size, structure, landscape context, and hydrological seasonality.
3. Using generalised linear models, we show that community-based fisheries management, which controls the density of apex predators, is the strongest predictor of phytoplankton biomass during the dry season, when lakes become discrete landscape units. Water transparency also emerges as an important bottom-up factor, but phosphorus, nitrogen and several lake and landscape metrics had minor or no effects on phytoplankton biomass. During the wet-season food pulse, when lakes become connected to adjacent water bodies and homogenise the landscape, only lake depth explained phytoplankton biomass.

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4. *Synthesis and applications.* Tropical freshwaters fisheries typically assume that fish biomass is controlled by bottom-up mechanisms, so that overexploitation of large predators would not affect overall ecosystem productivity. Our results, however, show that top-down forces are important drivers of primary productivity in tropical lakes, above and beyond the effects of bottom-up factors. This helps us to understand the enormous success of community-based 'fishing agreements' in the Amazon. Multiple stakeholders should embrace socio-ecological management practices that shape both bottom-up and top-down forces to ensure biodiversity protection, sustainable fisheries yields and food security for local communities and regional economies.

KEYWORDS

community-based management, flood pulse, food security, freshwater ecosystem, lake ecology, limnology, primary production, trophic cascade

1 | INTRODUCTION

Overfishing can affect the structure of entire food webs by (de)coupling key trophic linkages between resources and consumers (McCann et al., 2005). The impact of apex predators on producers has been investigated since the latter half of the 20th century (Hairston et al., 1960; Hodgson, 2005), resulting in the trophic cascade hypothesis which states that an increase in piscivorous fish depresses the biomass of planktivorous fish, increasing the biomass of herbivorous zooplankton which, in turn, reduces phytoplankton biomass (Carpenter et al., 1985). Many studies have validated this hypothesis in mesocosm and whole-lake experiments, and long-term studies in temperate regions (e.g. Brett & Goldman, 1996; Carpenter et al., 2011; Meijer et al., 1999; Mittelbach et al., 1995; Pace et al., 2013). However, investigations of top-down effects in tropical environments remain challenging, considering their sheer biological complexity, high prevalence of omnivory (González-Bergonzoni et al., 2012), high spatio-temporal variation in nutrient availability, landscape heterogeneity and fishing pressure, all of which can attenuate the magnitude or reverse the expected effects of trophic cascades (Hart, 2002; Van Leeuwen et al., 2007).

Phytoplankton provides a substantial contribution to primary production in aquatic ecosystems (Zwart et al., 2015), sustaining a network of trophic interactions, with decisive consequences for ecosystem functioning (Abonyi et al., 2018). The role of bottom-up factors influencing phytoplankton biomass has been studied for decades, but prevailing models developed in temperate zones may be inappropriate for tropical environments due to differences in food web configuration and varying amplitude of seasonal and interannual cycles (Huszar et al., 2006; Melack, 1976; Rugema et al., 2019; Sarmiento, 2012). Phytoplankton biomass is regulated by both top-down and bottom-up effects in temperate lakes distributed over a wide productivity gradient (Mazumder, 1994). The top-down effects were linked to food chain length (Hairston et al., 1960), which was indicated by the mean zooplankton size. Even-length food chains had larger zooplankton and lower chlorophyll *a* (*Chl-a*) to total phosphorus (TP) ratios whereas odd-length food chains had smaller zooplankton and higher *Chl-a*:TP ratios (see Hairston

et al., 1960). Similar analyses of Amazon floodplain lakes near Manaus indicated a general pattern of odd-length food chains and high *Chl-a* to total nutrient (TN) ratios (Trevisan & Forsberg, 2007). Phosphorus has been identified as the main limiting nutrient explaining most of the variation in phytoplankton biomass in temperate lakes in the northern hemisphere (Dillon & Rigler, 1974; Phillips et al., 2008). Nitrogen also appears to be an important predictor of phytoplankton biomass and production in some sub-tropical and tropical lakes (Forsberg et al., 2017; Trevisan & Forsberg, 2007; Xu et al., 2010). Other abiotic variables have been shown to influence phytoplankton dynamics, such as water transparency that can limit photosynthesis (Forsberg et al., 2017) and affect population growth by interfering in phytoplankton succession (Husman et al., 1999; Polimene et al., 2014). Additionally, macrophytes can interact with phytoplankton in complex ways, driving alternative phases of dominance (Asaeda et al., 2001; Goulder, 1969; Terborgh et al., 2018; Van Donk & Van de Bund, 2002) through asymmetric light inhibition, nutrient competition (Van Donk et al., 1993) and altered nitrogen availability due to denitrification (De Tezanos Pinto & O'Farrell, 2014; Weisner et al., 1994).

Physical attributes, such as landscape features, lake morphometrics and water column stratification can also play a substantial role in phytoplankton production by affecting bottom-up processes (Prepas et al., 2001; Sheffer & Van Nes, 2007; Søballe & Kimmel, 1987). In freshwater systems governed by the seasonality of the hydrological cycle, such as Amazonian floodplains, spatiotemporal changes in water bodies are particularly important, given that floodwater dynamics drastically controls nutrient cycles (Forsberg et al., 1988; Junk, 1997; Junk et al., 1989; Melack, 1976; Schmidt, 1973; Schönbrunner et al., 2012; Thomaz et al., 2007). During the high-water season, when floodplain lakes predominantly contain river water (Forsberg et al., 1988), phosphorus-rich river particles settle out of the water column, limiting phytoplankton photosynthesis and growth. At low water, these P-rich sediments are resuspended, elevating TP levels, *Chl-a* concentration and phytoplankton photosynthesis, while promoting N-limitation (Forsberg et al., Forsberg et al., 1988, 2017; Setaro & Melack, 1984). Although

sediment resuspension increases turbidity during low-water, algal blooms are often observed in Amazon floodplain lakes during this period (Abril et al., 2014; Amaral et al., 2018), and the phytoplankton community is dominated by species adapted to eutrophic and turbid environments, such as cyanobacteria that have large cell:bio-volume and therefore lower sedimentation rates (Lobo et al., 2018). Morphometric traits, including lake area, depth and shape are subjected to large seasonal variation that controls the nutrient resuspension dynamics, impacting ecological processes (Forsberg et al., 2017; Hakanson, 2005). Lake shape, for example, determines the fetch extent and therefore exposure to wind, which can effectively mix the water column. The frequency and the extent of water column mixing is depth dependent in Amazon floodplain lakes, and is directly related to the Amazon River hydrograph; minimum depths and high frequency mixing during low water and the opposite during high water (Forsberg et al., 2017; MacIntyre & Melack, 1984, 1988).

Innovative fisheries management practices in the Amazonian floodplains provide a unique opportunity for large-scale tests of the influence of top-down forces on tropical freshwater productivity. In most Amazonian floodplains, oxbow and other lakes become discrete landscape units during the dry season, providing attractive grounds for local fisheries. In response to unregulated large-scale commercial fisheries pressure, community-based management agreements result in spatial zoning of fishing access, which is the main and most effective community strategy to prevent overfishing, including arapaima (*Arapaima* sp.), a high-value apex-predator fish species (Campos-Silva et al., 2019; Campos-Silva & Peres, 2016; McGrath et al., 1993).

The effect of community-based protection has been remarkable, effectively protecting lakes hosting large populations of arapaima and other apex predators, including black caiman *Melanosuchus niger* and large catfishes (*siluriformes*). Conversely, top predator populations

are virtually nonexistent in unprotected lakes (Campos-Silva & Peres, 2016). Differences in fish community structure in protected and unprotected lakes create favourable conditions to investigate the effects of top-down versus bottom-up factors on phytoplankton biomass (Figure 1), which tends to be exceptionally variable in tropical environments (Sarmiento, 2012). Furthermore, understanding the drivers of phytoplankton productivity in Amazonian floodplains can help predict the dynamics of detritivore fishes, one of the most important functional groups for the subsistence economy of local Amazonian communities (Araujo-Lima et al., 1986; Batista et al., 1998; Begossi et al., 1999; Forsberg et al., 1993). This information could help environmental agencies and local communities design more effective fisheries management plans for these and other species (Forsberg et al., 1993).

Here we investigate the relative effects of top-down versus bottom-up forces—in terms of human exploitation versus nutrient and water transparency—in affecting phytoplankton biomass, while accounting for the influence of local and landscape heterogeneity. We sampled 58 lakes spread across ~600 km of fluvial distance along the Juruá River, during both the high-water and low-water seasons. Top-down force is determined by the protection status of each lake, a well-established proxy of top predator abundance in this Amazonian landscape (Campos-Silva & Peres, 2016), while bottom-up forces were represented by environmental variables including total phosphorus, total nitrogen, water transparency and macrophyte cover. The local (lake) and landscape metrics in our models included lake area, depth, shape, type, connectivity and distance to the main river channel. Our results show that community-based fisheries management exerts important influences on phytoplankton biomass. We discuss our findings in light of integrated bottom-up and top-down approaches to understand the primary productivity of tropical

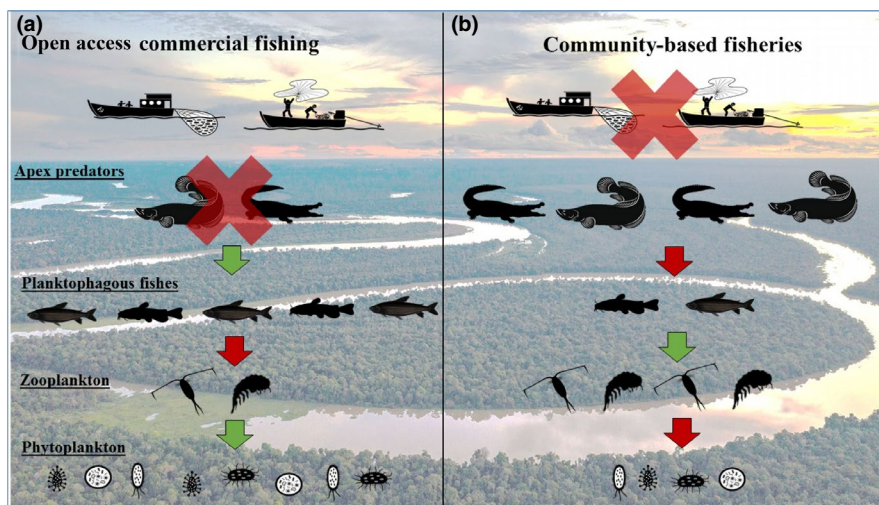


FIGURE 1 Infographic elucidating the potential effects of community-based fisheries management in the entire lake food web. In unprotected lakes (a), open access commercial fisheries are likely to exert strong exploitation pressure on fish stocks, often severely depleting populations of apex predators. In this context, planktivorous fish populations can increase, exerting pressure on zooplankton populations which subsequently decrease. Low zooplankton biomass can result in elevated phytoplankton biomass. Community-based fisheries management in turn (b) can ensure large apex predator population sizes, which can negatively impact planktivorous fish, boosting zooplankton but depressing phytoplankton biomass

environments, coupling baseline ecological variables with the imperatives of human exploitation in the same assessment.

2 | MATERIALS AND METHODS

2.1 | Study area

This study was carried out at 58 large floodplain lakes (mean dry-season area = 114.6 ± 129.2 ha) distributed within and outside two contiguous sustainable-use protected areas, which encompass 919,882 ha of upland and seasonally flooded forests along ~600 km of the Juruá River, a large meandering tributary of the Amazon River located in the central-western portion of the Amazon basin (Figure 2). The Juruá watershed is one of the principal sources of inorganic and organic matter for the Amazon lowlands (McClain & Naiman, 2008) and contributes high loads of suspended sediments associated with high turbidity and nutrient concentrations (Sioli, 1984).

The Juruá floodplain is governed by a pronounced annual flood pulse that often exceeds 10 m in amplitude (Hawes & Peres, 2016). Floodplain lakes were sampled during both the high-water (March–April 2014) and low-water periods (August–September 2014). There are two main lake types spread across the floodplain: oxbow lakes, formed through a complex process of meander cut-offs (Stølum, 1996), and ria lakes, which were formerly deeply incised river valleys, usually near upland forests (Bertani et al., 2015). Average lake depth was 11.8 ± 6.4 and 14.1 ± 6.5 m during the wet season, and 4.2 ± 3.4 and 6.7 ± 3.5 m during the dry season for oxbow and ria lakes respectively. Due to its high productivity, the Juruá River is one of the most important sources of fish traded across the Brazilian Amazon (Batista & Petrere Jr, 2003). This river also shows a pronounced

level of socio-political organisation, where local communities have been playing a central role in successful community-based arrangements that focus on aquatic resources (Campos-Silva & Peres, 2016; Campos-Silva et al., 2017, 2018).

2.2 | Fisheries management and top-down control

During the low-water season, Amazonian lakes become discrete landscape features, enabling no-take management based on the effective protection of floodplain lakes by excluding outside users. This management is organised around the concept of 'Fishing Accords' among all local communities from sustainable-use reserves, non-resident commercial fishers and the Fishermen Cooperative of Carauari (the nearest urban centre). For this study, we contrast two classes of lakes: Unprotected and Protected. Unprotected lakes include open-access lakes which are accessible to commercial fishing boats and subsistence-use lakes which are restricted to supplying local subsistence needs for the local community. In contrast, protected lakes exclude both commercial and subsistence fisheries but allow a sustainable harvest quota of arapaima in some managed lakes, once a year (see Campos-Silva & Peres, 2016). The effects of such fishing management on top predator levels have already been demonstrated (Campos-Silva & Peres, 2016). In some years, population size of giant arapaima (*Arapaima* sp.) was 30-fold higher in protected lakes when compared with unprotected lakes. However, in order to test the assumption that protected lakes hold a higher density of apex predators than unprotected lakes, we conducted a survey on giant arapaima *Arapaima* sp. during the dry season of 2014. Counts were based on standardised surveys, which were facilitated by the air-breathing of arapaima, whereby experienced fishermen can detect individuals as they break the water surface to breathe (see details in Castello, 2004).

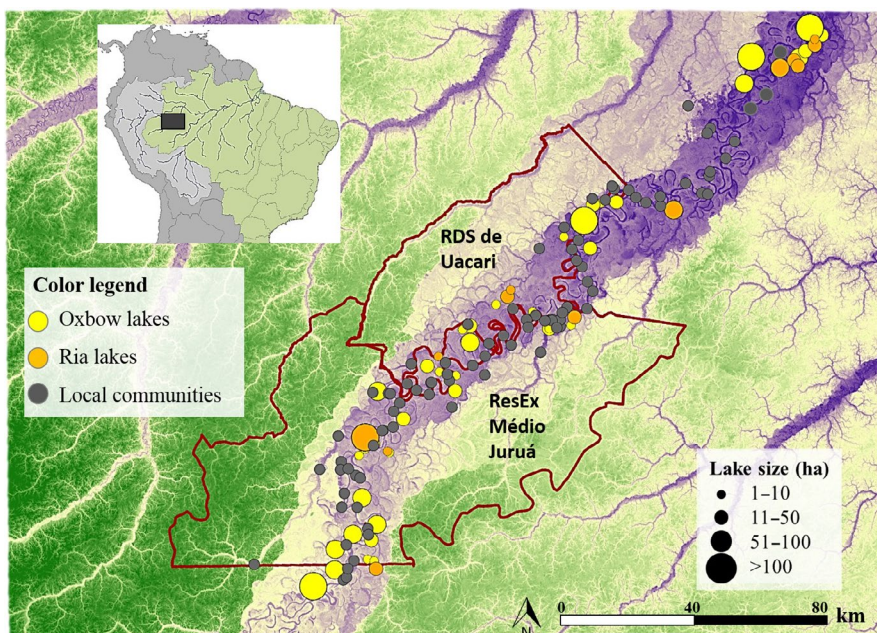


FIGURE 2 Geographic distribution of 58 floodplain lakes sampled across a ~600-km segment of the Juruá River of western Brazilian Amazonia. Yellow, orange and grey circles represent ria and oxbow study lakes and local communities respectively. Dark-red lines indicate the boundaries of two contiguous sustainable-use forest reserves, which amount to a combined area of 919,882 ha. Green and purple shading in the background represent elevation above sea level; the grey rectangle in the smaller inset map shows the extent of the entire study area. This map was generated in ArcGIS 10.3 (<http://www.esri.com>)

2.3 | Bottom-up control

Nutrient levels were determined from water samples collected on all lakes in April 2014 (wet season) and September 2014 (wet season). Total nitrogen (TN) and total phosphorus (TP) were determined using the simultaneous analysis method of Valderrama (1981) for both the high- and low-water seasons. Samples were first digested with a mixture of potassium peroxydisulphate, boric acid and sodium hydroxide in an autoclave. After digestion, P-PO₄ concentration was determined by light absorbance of ortho-molybdate blue at 882 nm and N-NO₃ was determined, following reduction with cadmium and addition of sulfanilamide/N-(1-naphthyl)-ethylenediamine dihydrochloride reagent, by light absorbance at 543 nm. Water transparency was estimated for each lake using the depth of the Secchi disk that was measured at a deeper portion of each lake during the high- and low-water seasons. Finally, lake macrophyte cover was initially mapped in the field and then independently estimated in ArcGIS (version 10.2) using 5-m resolution RapidEye[®] images from August to October 2013.

2.4 | Landscape and lake variables

Since Amazonian lakes are highly variable and inserted in different landscape contexts, our analyses contained several additional explanatory variables designed to control for such heterogeneity. Lake metrics were lake area, lake shape, lake depth, and lake type. Lake area was measured as the area (ha) of the water mirror. Shape index (SI) was measured as $SI = (P/200) \times (\pi A)^{0.5}$, where P is the lake perimeter and A is the lake area. SI represents the deviation from a perfect circle, for which a circular lake shows a maximum $SI = 1.0$ (Patton, 1975). Depth was defined as the maximum lake depth, measured in the field in each lake during both the high- and low-water seasons. Lake geomorphology was classified into two types: oxbow lakes and ria lakes. The landscape variables considered here were connectivity, which reflect if the lake is connected with the main river or not, and distance to river channel, estimated as the nearest Euclidian distance between the lake edge and the river channel. This variable is used as a proxy of time of isolation, since lakes near the river channel tend to be connected sooner during the high waters, exhibiting a shorter isolation period. All spatial metrics were extracted in ArcGIS 10.2 using classified RapidEye[®] images.

2.5 | Phytoplankton biomass estimates

We used Chl-*a* concentration as a proxy of phytoplankton biomass and productivity, but we note that primary productivity is a combination of metabolic and anabolic processes that we had not measured in this study. For Chl-*a* estimates, we sampled at the deepest point in each lake, during both the high- and low-water season. We first determined the extent of the euphotic zone, using the depth of a Secchi disk multiplied by a factor of 2.7 (Cole, 1994), and then

integrated the euphotic zone using a 20-L bucket and a vertical Van Dorn sampler (3 L). A 2-L water subsample was then transferred from the bucket to a polyethylene terephthalate (PET) bottle, which was stored on ice for subsequent determination of Chl-*a*, total phosphorus and nitrogen. For Chl-*a*, water samples were filtered through a GF/F glass fibre filter, after a time period, which never exceeded 8 hr after sampling. The concentration of Chl-*a* (µg/L) was determined spectrophotometrically, following sonication and overnight extraction in 90% acetone (10 ml) at 4°C. Chl-*a* extracts were subsequently centrifuged, decanted and read in a spectrophotometer in a 1-cm glass cuvette at 750, 664, 647, 630 nm. Chl-*a* concentration was then calculated with the tri-chromatic equations of Strickland and Parsons (1968). Filtration was conducted in a field laboratory in a diesel-powered boat under dim light. Filters were then frozen until further laboratory analysis (INPA, Manaus, Brazil) within a maximum of 8 weeks.

2.6 | Data analysis

We assessed seasonal changes in phytoplankton biomass by comparing the measurements of 41 lakes during the high- and low-water seasons using paired *t* tests. Differences in nutrient concentration (phosphorus and nitrogen) between seasons were also tested by paired *t* test, using a Bonferroni correction.

The assumption that population size of apex predators is driven by the protection status of the lakes was examined using a *t* test. We performed general linear models (GLMs) to examine the relative strength of top-down and bottom-up explanatory variables on phytoplankton biomass, controlling for lake and landscape metrics, for both low- (58 lakes) and high-water seasons (42 lakes). We used phytoplankton biomass as the dependent variable as a function of protection status (top-down), total phosphorus, total nitrogen, macrophyte cover (bottom-up), lake area, shape, depth and type (lake traits) and distance to river channel and connectivity (landscape trait) as explanatory variables. We initiated our analyses with simple variable models, followed by an analysis with the full model. We then followed a model selection approach. Models were fitted with lmer in the lme4 package and every model combination was examined using the MuMIn package (Barton, 2009) within the R platform (R Core Team, 2015).

We selected the most parsimonious models based on the lowest Akaike Information Criterion corrected for small sample sizes (AICc). $\Delta AICc$ was calculated as the difference between each model AICc and the lowest AICc, with a $\Delta AICc < 2$ interpreted as substantial support that the model belongs to the set of 'best' models. Akaike weights give the probability that a model is the 'best' model, given the data and the set of candidate models (Burnham & Anderson, 2002). Following model selection, we performed model averaging, which considers the beta average of all variables included in the most parsimonious models. Explanatory variables were z-standardised to allow comparisons among effect sizes. All assumptions were examined prior to analyses according to Zuur et al. (2010).

3 | RESULTS

The annual flood pulse of the Juruá floodplains strongly affected phytoplankton biomass and all bottom-up predictors measured (Figure 3). The average Chl-*a* concentration during the low-water season ($40.3 \pm 28.5 \mu\text{g/L}$) was more than 350 times higher than during the high-water season ($0.11 \pm 0.04 \mu\text{g/L}$, paired *t* test, $t = -8.19$, $p < 0.001$). The same pattern was found for total phosphorus concentration, which was higher during the low-water season ($2.6 \pm 1.1 \mu\text{M}$) compared to the high-water season ($1.7 \pm 2.1 \mu\text{M}$, $t = -2.99$, $p < 0.05$). An opposite pattern was found for total nitrogen, which was almost 30 times higher during the high-water season ($33.6 \pm 8.4 \mu\text{M}$) compared to the low-water season ($0.8 \pm 1.2 \mu\text{M}$, $t = 23.46$, $p < 0.001$).

As expected, the population size of giant arapaima was around 10-fold higher in protected lakes compared to unprotected lakes. The average number of individuals in protected and unprotected lakes was $108 (\pm 141.2 \text{ SD})$ and $18.9 (\pm 154 \text{ SD})$ respectively.

Considering explanatory variables independently, protection status emerged as the most important predictor of Chl-*a* concentration during the low-water season, ($\beta = -0.854 \pm 0.194$, $t = -4.403$, $p < 0.00001$, $r^2 = 0.26$), followed by water transparency ($\beta = 0.236 \pm 0.105$, $t = 2.256$, $p < 0.028$, $r^2 = 0.08$), and total phosphorus ($\beta = 0.218 \pm 0.105$, $t = 2.074$, $p < 0.028$, $r^2 = 0.07$), while the remaining variables were not significant. When all 11 explanatory variables were integrated into a full model, only protection status ($\beta = -0.857 \pm 0.210$, $t = -4.074$, $p = 0.0002$) and water transparency ($\beta = 0.319 \pm 0.096$, $t = 3.319$, $p = 0.0018$) emerged as significant independent variables, explaining half of the variation in Chl-*a* concentration across lakes ($r^2 = 0.50$, Table S2).

The model selection approach generated five plausible models for the low-water season, all of which contain protection status and water transparency (Table 1). The best model ($\Delta\text{AICc} = 0$) comprised of protection status, water transparency, macrophyte cover and phosphorus. Following model averaging, protection status had the strongest effect size in explaining Chl-*a* concentration in the low-water season ($\beta = -0.8 \pm 0.19$, Figure 4a), which indicates that protected lakes had lower concentrations of Chl-*a* (Figure 5a). The second strongest effect size was water transparency

($\beta = 0.39 \pm 0.09$, Figure 4a), showing a positive effect on Chl-*a* concentration (Figure 5b). Total phosphorus, lake depth and macrophyte cover were also present in parsimonious models, but showing no significant effect size during the low-water season.

During the high-water season, community-based fisheries management was discontinued and the landscape became more homogeneous. In simple models, lake depth was the only factor explaining Chl-*a* concentration ($\beta = -0.016 \pm 0.005$, $t = -3.133$, $p = 0.003$, $r^2 = 0.21$). In the full model, none of the explanatory variables significantly affected Chl-*a* concentration (Table S2). The model selection approach generated five acceptable models for the low-water season, all of which containing lake depth (Table 1). Moreover, the best selected model contained only lake depth. In the model averaging approach, only lake depth had a significant effect size during the high-water season with deeper lakes exhibiting a lower concentration of Chl-*a* (Figure 4b). Distance to the main river channel, water transparency, lake shape and phosphorus concentration were also present among the parsimonious models, but with non-significant effect sizes.

4 | DISCUSSION

A hegemonic paradigm considers fish yields to result primarily from ecosystem productivity (Junk et al., 1989; Malick et al., 2015; Melack, 1976; Runge, 1988). The opposite pathway—in which large-scale variation in fish communities can explain the variance in primary productivity via top-down processes—has been poorly acknowledged due to the lack of large-scale experimental evidence. Here we show evidence of top-down forces in a complex tropical ecosystem due to a unique opportunity made possible by innovative (and often hard-fought) local fisheries management agreements. We show that top-down effects on phytoplankton productivity can be an important component above and beyond widely acknowledged bottom-up forces that modulate the productivity of complex tropical lakes systems (Lowe-McConnell, 1987). The annual flood pulse in white-water Amazonian floodplains leads to a large regime change across the landscape, which ensures that different mechanisms drive phytoplankton biomass according to seasonal changes in

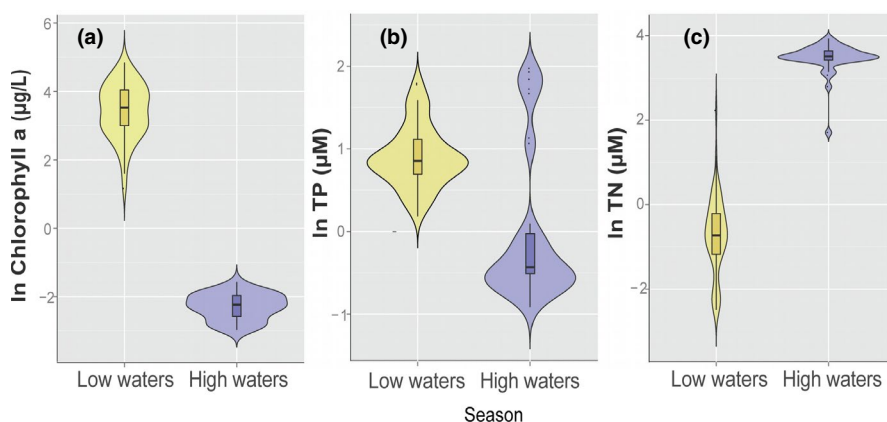


FIGURE 3 Violin boxplot of (a) Chl-*a* concentration, (b) total phosphorus, and (c) total nitrogen during the low-water and high-water season for 58 lakes across ~600 km along the Juruá River

TABLE 1 Full list of parsimonious models for high and low-water season

| Models low water season | β Management class | β Macrophyte coverage | β Water transparency | β Phosphorus | β Depth | df | logLik | AICc | delta AICc | Weight | r-squared |
|--|--------------------------|--------------------------------|----------------------------|--------------------|----------------|----|---------|--------|------------|--------|-----------|
| Management class + macrophyte coverage + Water transparency + Phosphorus | -0.87 ± 0.18 | -0.16 ± 0.1 | 0.34 ± 0.1 | 0.15 ± 0.1 | | 6 | -53.371 | 120.4 | 0 | 0.042 | 0.44 |
| Management class + macrophyte coverage + Water transparency | -0.96 ± 0.14 | -0.15 ± 0.1 | 0.31 ± 0.18 | | | 5 | -54.904 | 121 | 0.57 | 0.032 | 0.41 |
| Management class + Water transparency + Phosphorus | -0.82 ± 0.19 | | 0.30 ± 0.1 | 0.15 ± 0.1 | | 5 | -55.091 | 121.3 | 0.95 | 0.026 | 0.4 |
| Management class + depth + macrophyte coverage + Water transparency + Phosphorus | -0.85 ± 0.18 | -0.16 ± 0.1 | 0.32 ± 0.1 | 0.16 ± 0.1 | 0.10 ± 0.1 | 7 | -52.619 | 121.5 | 1.09 | 0.025 | 0.45 |
| Management class + Water transparency | -0.91 ± 0.18 | | 0.28 ± 0.1 | | | 4 | -56.456 | 121.7 | 1.28 | 0.022 | 0.37 |
| Models high water season | β Depth | β Distance to main river | β Water transparency | β Phosphorus | β Shape | df | logLik | AICc | delta AICc | Weight | r-squared |
| Depth | -0.02 ± 0.005 | | | | | 3 | 85.136 | -163.6 | 0 | 0.062 | 0.21 |
| Depth + Distance to main river | -0.02 ± 0.005 | -0.01 ± 0.005 | | | | 4 | 85.99 | -162.9 | 0.75 | 0.042 | 0.24 |
| Depth + Water transparency | -0.01 ± 0.005 | | -0.01 ± 0.005 | | | 4 | 85.883 | -162.7 | 0.97 | 0.038 | 0.23 |
| Depth + Shape | -0.02 ± 0.005 | | | 0.005 ± 0.005 | | 4 | 85.829 | -162.5 | 1.08 | 0.036 | 0.23 |
| Depth + Phosphorus | -0.01 ± 0.005 | | | -0.004 ± 0.005 | | 4 | 85.572 | -162 | 1.59 | 0.028 | 0.22 |

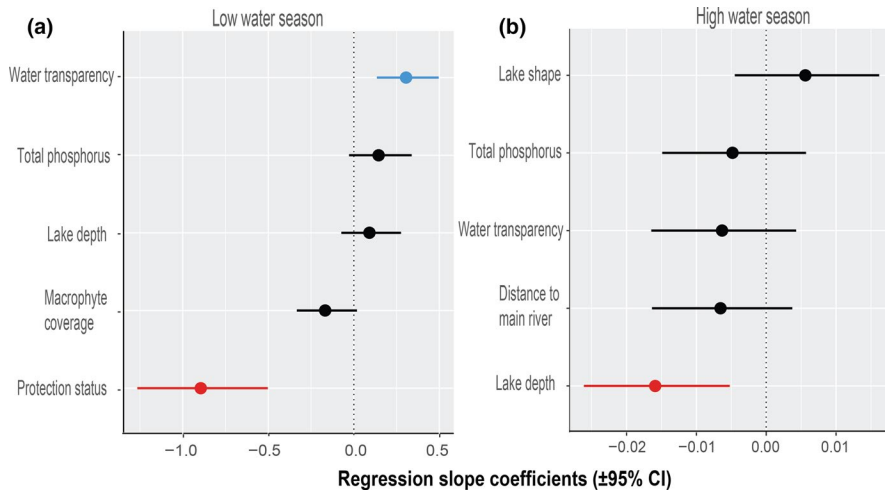


FIGURE 4 Estimates for regression slopes ($\pm 95\%$ confidence intervals, CIs) showing the magnitude and direction of the effects of different variables on Chl-*a* (~phytoplankton biomass) within 58 floodplain lakes sampled in the western Brazilian Amazon. Solid circles indicate the mean estimates and horizontal lines indicate confidence intervals. For significant variables, CIs do not cross the horizontal dotted line at zero. Blue and red symbols represent positive and negative effects respectively. Boxes *a* and *b* represent the low-water and high-water seasons respectively

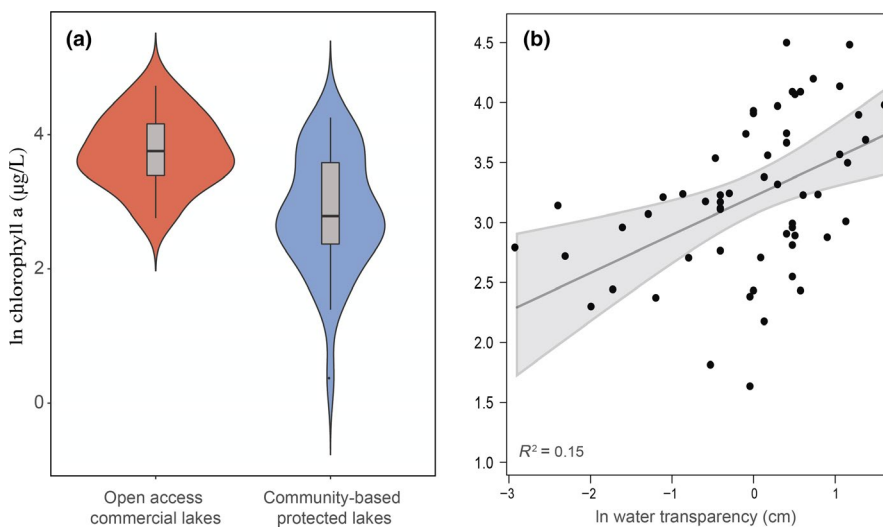


FIGURE 5 Partial regression of phytoplankton biomass (measured as Chl-*a*) during the low-water season as a function of (a) lake protection status (open access to commercial fishing in red; protected lakes in blue) and (b) water transparency (depth measurements in cm using a Secchi disc)

water level. During the wet season, the system was homogenised by the prolonged annual flood pulse and only lake depth was an important correlate of Chl-*a* concentration. During the low-water season, however, community-based fisheries management became the most important factor explaining Chl-*a* concentration, followed by water transparency.

Few studies have attempted to understand the effect of apex predators on the biomass of primary producers at large spatial scales, especially in tropical environments (Borer et al., 2005; Brett & Goldman, 1996; Hodgson, 2005). In part, the paucity of information on tropical freshwater systems results from their complexity including high habitat diversity, difficult access, high spatial heterogeneity, breadth in resource spectra and the physiology of organisms, and most of these factors are important in understanding the magnitude of top-down control on producer biomass (Borer et al., 2005). Since the conceptual framework proposed by Carpenter and Kitchell (1993), several studies have corroborated the trophic cascade hypothesis (Carpenter et al., 2011; Flecker & Townsend, 1994; Polis, 1994; Strong, 1992). Although trophic cascades vary widely in their effects, they apply to many types of environments (Shurin et al., 2002). In long-term

experiments, for example, the reintroduction or eradication of piscivorous fish induces drastic changes in planktivorous fish abundance, resulting in substantial changes in lower trophic levels (Carpenter et al., 2011; Mittelbach et al., 1995; Pace et al., 2013). Our study indicates that protected lakes, under a tight community-based governance agreement, retain large populations of apex predators that, in turn, can exert a considerable indirect effect on phytoplankton biomass (Figure 1), presumably by reducing the biomass of zooplanktivorous fish which allows zooplankton numbers to increase thereby reducing phytoplankton biomass. The inverse trend can occur in open access lakes subject to intensive commercial fishing pressure, where the lack of apex predators presumably resulted in a higher biomass of zooplanktivorous fish, lower zooplankton abundance and higher levels of Chl-*a*. Previous results from floodplain lakes near Manaus also support this interpretation (Trevisan & Forsberg, 2007). The populations of large iconic predatory fish species, such as *Arapaima* spp., are also greatly reduced in these open access commercial lakes due to intensive fishing pressure (Castello et al., 2015). This has resulted in higher populations of small zooplanktivorous species, as evidenced by the small average size (<0.5 mm) of zooplankton and

high Chl-*a* yields in these systems (Trevisan & Forsberg, 2007), similar to those observed in our open access lakes. The relationship between piscivorous fish and limnological parameters was also reported in other studies. Water transparency, controlled by depth and lake area, was strongly correlated with piscivorous fish density in Orinoco floodplain lakes (Rodríguez & Lewis Jr, 1997). These systems are probably very similar to Amazonian floodplains, with a compressed food web resulting from intensive top-down control in which fish consumption depends of trophic levels 1 and 2 (Lewis Jr et al., 2001).

The trophic cascade hypothesis has also been the target of some criticism. Indeed, some studies have shown that changes in food web structure are accompanied by several compensatory mechanisms, so that the trophic cascade hypothesis would be too simplistic to describe this complexity in the long term (Hodgson, 2005; Persson, 1999). Manipulative experiments have highlighted that shifts in predator abundance can modify rates of herbivory causing changes in nutrient recycling through excretion, for example, which can have a strong influence on producer dynamics (Vanni & Findlay, 1990; Vanni & Layne, 1997). Therefore, the details of the mechanisms behind the trophic cascade hypothesis are at best complex and still not fully understood, but it is clear that the presence of higher trophic levels strongly influences producers in many environments, explaining a large part of the variance that remains unexplained by bottom-up approaches alone (Hodgson, 2005).

There is a vast literature about how bottom-up factors control phytoplankton biomass. Phosphorus is often the main limiting factor (Schindler, 1978; Tilzer, 1990; Vollenweider & Kerekes, 1980), but nitrogen may play a central role in some tropical environments (Lewis, 2010; Thornton, 1987; Trevisan & Forsberg, 2007). Although marginally significant, our findings suggest that phosphorus can contribute to phytoplankton biomass production, but only during the dry season. Nitrogen did not appear to be an important driver of phytoplankton biomass and production at Juruá lakes, but it has been shown to be important in other white- and black-water drainages in the Amazon (Forsberg et al., 2017; Trevisan & Forsberg, 2007). Variations in lake depth was the main factor affecting Chl-*a* concentration during the high-water period, presumably due to its direct effect on TP that limits phytoplankton biomass. During this period, the Juruá and other large tributaries of the Amazon flood vast areas of lateral floodplains, creating a mosaic of aquatic habitats, including flooded forests, herbaceous plants, side channels and open-water areas (Junk et al., 1989; Melack & Hess, 2010). River-borne sediments, which are the main source of phosphorus in Amazonian floodplain lakes, settle out of the water column at this time (Forsberg et al., 1988), causing phosphorus limitation to phytoplankton growth (Forsberg et al., 2017). Water columns are generally stratified during this period (Melack & Fisher, 1990; MacIntyre & Melack, 1988) favouring nutrient segregation (Forsberg et al., 2017), with concomitant increase in water transparency, compared to the low-water period (Forsberg et al., 2017). Given the strong evidence for phosphorus limitation

during this period (Forsberg et al., 2017; Setaro & Melack, 1984), the lack of a correlation between Chl-*a* and TP was surprising and suggests the importance of other mechanisms explaining Chl-*a* variability that were not covered in this study.

Vertical mixing is an important depth and fetches a dependent mechanism (MacIntyre & Melack, 1988) that impacts nutrient dynamics (Forsberg et al., 1988; Melack & Fisher, 1990) and planktonic primary production in Amazonian floodplain lakes (Amaral et al., 2018; Forsberg et al., 2017). Based on hundreds of temperature profiles measurements taken at dawn (06:00 hr) in a central Amazon floodplain lake, MacIntyre and Melack (1988) described that full vertical mixing is common in lakes shallower than 4 m, whereas stratification tends to persist for longer periods in deeper lakes (>6 m). Unfortunately, we did not measure water column temperature profiles to assess stratification in this study, but we can make some inferences of its effect on nutrient dynamics and Chl-*a* biomass by considering variation in these variables and water transparency, and comparing their values across periods and lake depths (MacIntyre & Melack, 1988). During the low-water period, Secchi disc depth was positively correlated with Chl-*a*. Since most lakes in this study were shallower than 4 m during this period, daily vertical mixing may have led to sediment resuspension, increasing phosphorus availability for phytoplankton growth (Forsberg et al., 1988, 2017). Since lake water transparency is also an important limiting factor for phytoplankton growth in the Amazon (e.g. Forsberg et al., 2017), it is reasonable to expect that higher transparency would boost Chl-*a* biomass, assuming phosphorus inputs from the sediments in lakes shallower than 4 m were fully mixed. To test an alternative effect of phosphorus limitation for phytoplankton growth during low-water, we compared the mean phosphorus concentration at lakes shallower than 4m with deeper lakes (MacIntyre & Melack, 1984, 1988). Although no significant differences could be found between these groups, mean TP concentration was 12% lower in deeper lakes. Conversely, during the high-water period, most lakes were deeper than 6 m, and therefore likely to be stratified (MacIntyre & Melack, 1984, 1988), and water transparency tended to increase. These observations corroborate the previously described mechanism of phosphorous limitation associated with sediment settling when lake depth increases (Forsberg et al., 1988), although we have detected a reduction in water transparency for a subset of lakes during the high-water period.

Vertical mixing in tropical lakes is very dynamic, and the depth of the actively mixing layer can range widely over 24 hr (e.g. Barbosa & Padisák, 2002; Rugema et al., 2019), as a function of water column heating due to solar radiation incidence, causing the actively mix layer depth to be shallower around noon (Amaral et al., 2018; MacIntyre & Melack, 1984). These daily vertical movements were shown to affect nutrients (Melack & Fisher, 1990) and greenhouse gases dynamics (Amaral et al., 2018, 2020; Barbosa et al., 2020), but the impact to phytoplankton biomass and primary production on Amazon floodplain lakes are yet to be assessed. We recommend that future studies should focus on seasonal temperature

profile data, in combination with nutrients measurements, *Chl-a*, and direct estimates of primary productivity rates (e.g. incubations or free water measurements) to better assess the impacts of vertical mixing on primary production in Amazon lakes. Additionally, during the high-water period, water currents can affect stratification and cause vertical mixing, a mechanism that is yet to be investigated in detail.

4.1 | Flood pulse as a system reset

The vast amount and extent of floodwaters during the persistent flood pulse of 10–12 m over >6 months of the year exerts a marked dilution effect on lake limnology. This alters not only phytoplankton biomass, but also the structure and composition of the entire community assemblage (De Emiliani, 1997; de Melo et al., 2019; Huszar & Reynolds, 1997). The inundation period can thus be understood as a 'system reset', which can lead to substantial homogenisation of biological communities. Following this inundation period, however, biological communities are reconstituted into units that are exposed to a wide array of driving forces (Junk et al., 1989). In the case of phytoplankton, fisheries management and water transparency had the strongest positive effects on phytoplankton biomass, overriding the effects of all other variables. Future studies should attempt to understand how the trophic cascade hypothesis works over long time-scales, given that prolonged dilution events brought about by the annual flood pulse radically alter all lake limnology properties. Additional efforts to understand lake mixing are needed since it drives sediment resuspension that affects water transparency and ultimately *Chl-a* concentration.

4.2 | Implication for conservation of tropical freshwater environments

The human exploitation footprint has reached even some of Earth's most isolated freshwater systems. Commercial fishing, even if deployed through a large fleet of dugout canoes and small boats, can have drastic impacts on inland aquatic ecosystems, altering all trophic levels. These findings challenge the overall view which states that, due to the immense scale and dynamic of the Amazonian freshwater systems, fish productivity is exclusively controlled by bottom-up forces. In fact, during the dry season, exactly when fishing activities are more intense, top-down forces predominate. Our findings reinforce the importance of including human resource exploitation into ecosystem assessments, even in remote and sparsely settled areas. We highlight the complexities involved in adequately managing such complex and dynamic systems. By elucidating the primary drivers of *Chl-a* concentration as a proxy of primary production, fisheries management can be effectively informed, so that local to regional stakeholders can increase the transfer of auto-trophic energy through fish food chains and maximise yields. While this study advances on such endeavour, future studies should focus

on robust sampling of all components of food webs in Amazonian lakes to further elucidate the effects of top predator abundance on different trophic levels.

The results also help us to understand the success of the innovative participatory fishing accords in Amazon, which are used as a conservation tool to negotiate the access to lakes and aquatic resources between local communities and professional fishers, delivering food and economic security for rural communities. Such agreements usually establish three categories of lake resource access: (a) Protected lakes, where all types of fishing are prohibited. In some of these lakes (locally called 'management lakes'), a sustainable arapaima cull is permitted once each year; (b) subsistence lakes, designed to supply food for local dwellers, where only rural communities responsible for protecting that lake can fish and (c) open-access lakes, which can be accessed by commercial fishing boats. Our findings show that this is a rare win-win arrangement, where protected lakes can host large population of high-value species, and open-access lakes can host large biomass of phytoplankton, which in turn can ensure a high biomass of detritivorous fish that plays a central role in local subsistence. This model can be scaled up to other major river basins, ensuring biodiversity protection and maximising yields of target species for food security of rural communities.

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AUTHORS' CONTRIBUTIONS

J.V.C.-S., C.A.P. and J.H.F.A. designed the experiment; J.V.C.-S. and C.A.P. collected the data; J.V.C.-S., C.A.P., J.H.F.A., H.S. and C.R.F. analysed the data and J.V.C.-S., C.A.P., J.H.F.A., H.S., B.F. and C.R.F. co-wrote the manuscript. All authors approved the final version of the manuscript.

DATA AVAILABILITY STATEMENT

Data are available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.15dv41nw0> (Campos-Silva & Peres, 2020).

ORCID

João Vitor Campos-Silva  <https://orcid.org/0000-0003-4998-7216>

Carlos A. Peres  <https://orcid.org/0000-0002-1588-8765>

João Henrique Fernandes Amaral  <https://orcid.org/0000-0002-8992-6082>

Hugo Sarmiento  <https://orcid.org/0000-0001-5220-7992>

Bruce Forsberg  <https://orcid.org/0000-0001-7606-0585>

Carlos Roberto Fonseca  <https://orcid.org/0000-0003-0292-0399>

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SUPPORTING INFORMATION

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