EVALUATING THE INFLUENCE OF LAND USE, LANDSCAPE PROPERTIES, PRECIPITATION AND FISH ON AQUATIC ECOSYSTEM FUNCTIONING AND BIODIVERSITY THROUGH LARGE TEMPORAL AND SPATIAL SCALE ASSESSMENTS ACROSS LAKES AND RESERVOIRS

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CENTRO DE BIOCIÊNCIAS

DEPARTAMENTO DE ECOLOGIA

PROGRAMA DE PÓS GRADUAÇÃO EM ECOLOGIA

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Orientador(a): Dra. Luciana da Silva Carneiro

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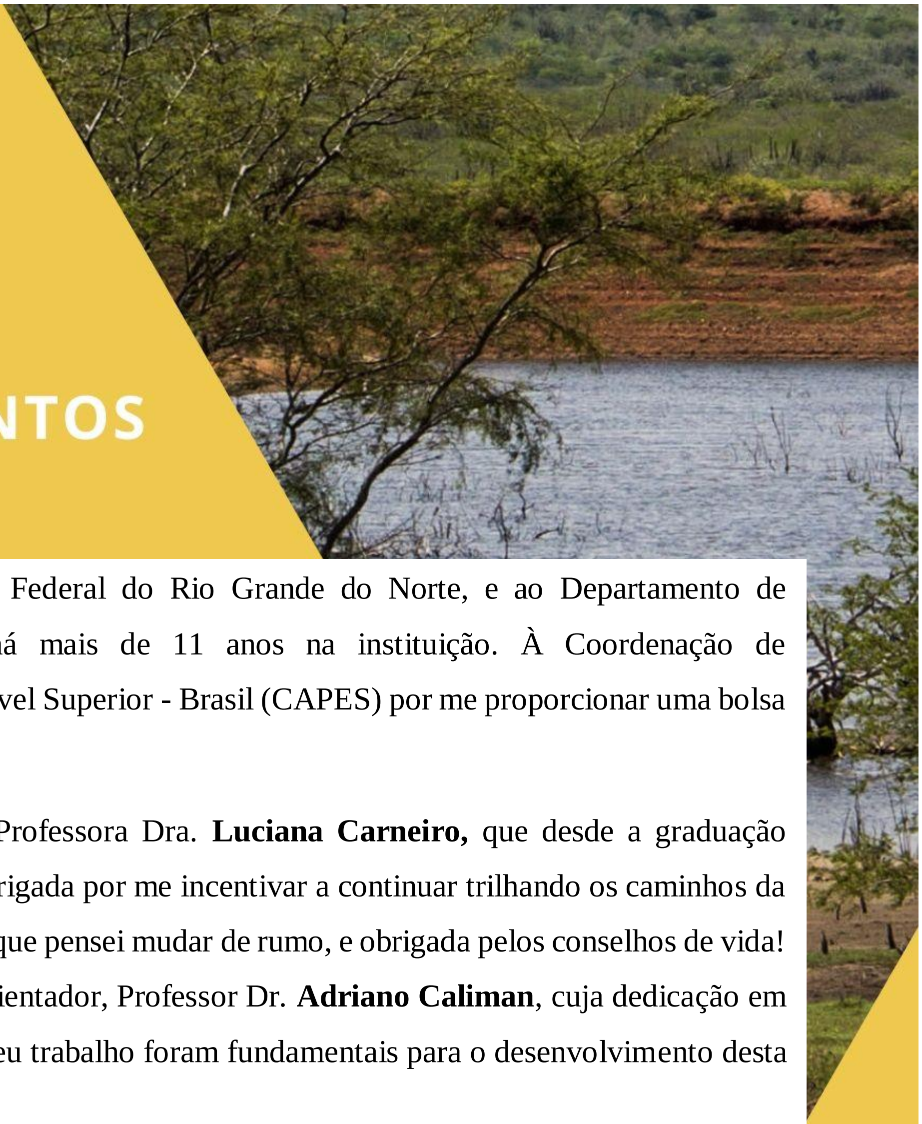

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ABSTRACT: Nutrient cycling is a fundamental ecosystem service as it provides an adequate balance of elements that are necessary for life. In freshwaters, the balance of nitrogen (N) and phosphorus (P) are of special interest as they often limit or control primary production and biomass formation. While the availability of these nutrients is fundamental for the maintenance of biodiversity and productivity of freshwaters, their excess can lead to eutrophic conditions that are associated with impaired water quality and biodiversity loss. The nutrient balance in freshwaters can potentially be affected by a variety of biotic and abiotic, external and internal pathways. In this thesis, two frameworks were explored. First, a spatial framework focused on external processes, where we investigated the direct and indirect effects that land use (i.e. type, extent), precipitation and landscape properties (i.e. lake origin, lake and catchment absolute and relative size and geomorphology) have on biotic and abiotic properties of freshwater systems. More specifically, in chapter one we evaluated, across 98 tropical lakes and reservoirs, the individual and interactive effects of land use, precipitation and landscape properties on patterns of water quality parameters (N, P and chlorophyll-*a*). In chapter two, we characterized the 98 lakes as natural or artificial and compared them regarding the landscape properties of their surroundings, their morphometry, and their physico/chemical characteristics to verify whether those factors can be associated with average patterns of phytoplankton community structure at both local and regional scales. The second approach, presented in Chapter 3, was a long-term temporal framework focused on internal processes related to nutrient cycling where we assessed whether an omnivorous fish with high biomass and growth rate is a source or sink of N and P to the pelagic zone of a temperate eutrophic lake, at various time scales ranging from days to 20 years.

Key-words: nutrient cycling, land use, allochthonous subsidies, nonpoint source pollution, fish carcass, eutrophication, biodiversity

AVALIANDO OS EFEITOS DE PROPRIEDADES DO USO DO SOLO E DA PAISAGEM, DO CLIMA E DE PEIXES NO FUNCIONAMENTO E BIODIVERSIDADE DE ECOSSISTEMAS AQUÁTICOS AO LONGO DE LARGAS ESCALAS ESPAÇO-TEMPORAIS EM LAGOS E RESERVATÓRIOS

RESUMO: A ciclagem de nutrientes é um serviço ecossistêmico fundamental, pois proporciona um equilíbrio adequado dos elementos necessários à vida. Nos ecossistemas de água doce, o balanço de nitrogênio (N) e fósforo (P) é de especial interesse, pois frequentemente estes elementos limitam ou controlam a produção primária e a formação de biomassa. Embora a disponibilidade desses nutrientes seja fundamental para a manutenção da biodiversidade e produtividade dos ecossistemas limnéticos, seu excesso pode levar a condições de eutrofização que estão associadas à deterioração da qualidade da água e à perda de biodiversidade. O balanço de nutrientes nos sistemas de água doce pode ser potencialmente afetado por uma variedade de vias bióticas e abióticas, externas e internas. Nesta tese, duas abordagens foram exploradas, uma abordagem espacial, focada em processos externos, onde foram investigados os efeitos diretos e indiretos do uso da terra (i.e. tipo, extensão), precipitação e propriedades da paisagem (tamanho absoluto e relativo e geomorfologia do lago e bacia) nas propriedades bióticas e abióticas de ecossistemas aquáticos. Mais especificamente, no capítulo um, avaliamos em 98 lagos e reservatórios tropicais os efeitos individuais e interativos do uso da terra, precipitação e propriedades da paisagem sobre parâmetros relacionados à qualidade da água (N, P e clorofila-a). No capítulo dois, caracterizamos os 98 lagos como naturais ou artificiais e os comparamos em relação às propriedades da paisagem em seu entorno, sua morfometria e suas características físico-químicas para verificar se esses fatores podem ser associados a padrões médios da estrutura da comunidade fitoplanctônica em escalas locais e regionais. A segunda, é uma abordagem temporal de longo prazo, focada em processos internos relacionados ao ciclo de nutrientes, onde avaliamos se um peixe onívoro com alta biomassa e alta taxa de crescimento é uma fonte ou sumidouro de N e P para a zona pelágica de um lago temperado eutrófico em várias escalas de tempo variando de dias a anos.

Palavras – chave: Ciclagem de nutrientes, uso do solo, subsídios alóctones, fontes não pontuais de poluição, carcaças de peixes, eutrofização, biodiversidade

EVALUATING THE INFLUENCE OF LAND USE, LANDSCAPE PROPERTIES, CLIMATE AND FISH ON AQUATIC ECOSYSTEM FUNCTIONING AND BIODIVERSITY THROUGH LARGE TEMPORAL AND SPATIAL SCALE ASSESSMENTS ACROSS LAKES AND RESERVOIRS

GENERAL INTRODUCTION

Nutrient cycling, i.e. the flux of nutrients between organisms, habitats or ecosystems is a fundamental ecosystem service as it provides an adequate balance of elements that are necessary for life (Vanni, 2002). In freshwaters, the research on nutrients balance is mainly focused on nitrogen (N) and phosphorus (P) as the supply rate of this key elements often limits or control primary production and biomass formation (Paerl, 2009). An adequate balance of nutrients is fundamental for the maintenance of productivity, resources availability and biodiversity of freshwaters, while the excess of nutrients can lead to eutrophic conditions that are associated with increased phytoplankton biomass, the abundance of nuisance and toxic algae, increased water turbidity, oxygen depletion and fish deaths, impairing freshwater quality and compromising its biodiversity and economic value (Carpenter et al., 1998; Catherine et al., 2010).

Ecosystems are connected by spatial flows of matter, energy and organisms across their physical boundaries (Elton 1927, Polis & Hurd, 1995; Loreau, Mouquet and Holt 2003, Ballinger & Lake, 2006; Gratton, Donaldson & Zanden, 2008). A great proportion of ecosystems are thus subsidized *via* external processes. Freshwaters are especially subject to allochthonous subsidies because of gravity and its concave profiles in the landscape, which enables the flux of materials from the catchment areas into the water bodies (Vanni et al., 2005; Vannote et al., 1980). The role of internal processes on nutrient cycling *via* animals (e.g. fish) has also been well documented, once animals consume, store, release and translocate nutrients at multiple scales, and at ecologically relevant rates, having potential to affect nutrient cycling, water quality and ecosystem productivity (Barton et al., 2013; Beasley et al., 2012; Subalusky and Post, 2018; Vanni, 2002; Vanni et al., 2006; Williamson et al., 2018). Thus, nutrient balance in freshwater systems can be affected by a variety of internal and external processes (Table 1).

In this thesis, two frameworks were explored. The first one is a spatial framework focused on external processes, where we investigated the individual and interactive effects of land use (i.e. type, proximity and extent) landscape properties (i.e. lake origin, lake and catchment absolute and relative size and geomorphology) and precipitation on water quality indicators and on local and regional taxonomic phytoplankton diversity, by using a dataset of 98 perennial natural lakes and reservoirs (hereafter in this section, lakes) located in Rio Grande do Norte, northeast Brazil. Their location expands from the coastal to the semi-arid region, with climate varying from humid to semi-arid and trophic conditions varying from oligotrophic to hypereutrophic. Furthermore, these 98 lakes are included in different contexts of land occupation and use, from pristine areas to urban concentrations, farming and livestock production areas, among others (Cabral et al., 2019; Junger et al., 2019).

The second approach is a temporal framework focused on internal processes related to nutrient cycling where we assess whether and how the long-term variation of population dynamics of an omnivorous fish with high biomass and growth rate act as a source or sink of N and P to the pelagic zone of a temperate eutrophic lake, at various time scales ranging from days to years. To accomplish this, we used a population-level model for gizzard shad (*Dorosoma cepedianum*) over a 20-year period in Acton Lake, a eutrophic reservoir in southwest Ohio, U.S.A (Williamson et al., 2018).

I.I External Process - The influence of catchment land use and its interactions with lake and landscape properties and precipitation

Earth’s surface has experienced large scale transitions from natural landscapes to altered land covers, through the creation and expansion of urban areas and the conversion of pristine lands to agriculture, pasture, and urban landscapes (Foley et al., 2005; Seto et al., 2012). Agriculture and urbanization are amongst the most intensive types of land use. As of 2015, farming lands alone, occupy a combined area of approximately 34% of the Earth’s ice free land surface (Carpenter et al., 2011; Ramankutty et al., 2008) overlapping the amount of forested areas (about 31%), while urban areas covered about 2.85% of land surface (The World Bank, 2019).

Over the past years, the impacts of human alterations on natural environments have become a rising research topic on environmental sciences because of the growing recognition of the adverse effects of land use on global ecosystems. Thus, anthropogenic land uses represent a potential threat to the provisioning and maintenance of ecosystem services and functions. Particularly, recent studies have shown an intimate relationship between the development of anthropogenic land use types and impaired water quality (Doubek et al., 2015; Jeppesen et al., 1999; Wang et al., 2008).

Agriculture and urban impervious surfaces are one of the primary sources of N and P to freshwaters (Paul and Meyer, 2008; Vanni et al., 2011). This artificial enrichment of N and P is the main threat to water quality worldwide (Carpenter et al., 2011) causing severe problems as toxic algal blooms, reduced oxygen on water column, fish death among others. These nutrients come from sewages, fertilizers, pesticides and detergents. Thus, land use can be a major factor controlling the export of nutrients from the catchment of inland aquatic systems, inducing changes in resources availability and nutrient ratios entering freshwaters, thus potentially affecting water quality and provoking changes in freshwater communities.

The effects of lands use on water quality and biodiversity can be better understood when combined with complementary environmental parameters such as climatic and morphometric variables (Bucak et al., 2018; Catherine et al., 2010; Knoll et al., 2015). Landscape properties such as topography (i.e. declivity), the absolute and relative size of catchments and their lakes (Bremigan et al., 2008; Hayes et al., 2015; Vannote et al., 1980) and the origin (i.e. natural or artificial) of the aquatic systems (Dodson et al., 2006; Nielsen et al., 2012) are factors that can influence the transport rates of allochthonous material to waterbodies, as well as determine how sensible these systems are to external inputs of materials.

For instance, differences in lake morphometry can arise when the waterbodies are originated from different processes, such as natural lakes and reservoirs. While natural lakes are created from geologic time and forces (Thornton, 1984), reservoirs are newer ecosystems constructed in its majority in the last 60 years aiming to store water for multiple purposes (Soballe and Kimmel, 1987; Thornton, 1984). Compared to lakes, reservoirs usually present greater catchment size because dams are strategically built along higher order rivers to allow damming of water from a large catchment area. Reservoirs are also built in places with more rugged topography, and therefore, they usually also present higher depths (thus, greater volume), perimeter and consequently higher catchment area to lake volume (CA:LV) and perimeter to lake volume (LP:LV) ratios. Those features can lead to a higher potential influence from allochthonous materials entering the reservoirs (Doubek and Carey, 2017; Knoll et al., 2015; Menezes et al., 2018; Thornton, 1984), which in turn can affect lake productivity and alter patterns of local and regional plankton diversity (e.g. species richness, abundance and composition) (Cabral et al., 2019; Doubek et al., 2015; Mantzouki et al., 2015; Schindler, 2006).

Additionally, climatic characteristics such as the patterns of precipitation can also interact with landscape properties and land use to affect water quality and biodiversity. For instance, the magnitude and variability of precipitation can interfere by intensifying (e.g. via soil percolation or surface runoff) or attenuating (e.g. via dilution) the land use effects on aquatic systems (Jeppesen et al., 2015). Thus, the interaction of these factors (land use, lake and landscape properties, precipitation) can reflect on the concentration of nutrients in the water which will affect its quality and the aquatic ecosystem productivity and biodiversity.

I.II Internal Process – the role of fish as source or sink of nutrients

Differently from allochthonous inputs of nutrients to water bodies, which are strictly sources of nutrients, animals, like fish can act as sources or sinks of nutrients at the ecosystem scale. A fish population can act as a source of nutrients when it is releasing nutrients in available forms to other members of the ecosystem, and as a sink when they are removing nutrients from the circulation in the ecosystem (Kitchell et al., 1975; Vanni et al., 2013). Most studies on nutrient cycling by fish (and other aquatic animals) have focused mostly on their role as a nutrient source, mainly through excretion (Atkinson et al., 2017; Subalusky and Post, 2018). However, because fish can represent a large proportion of animal biomass in many ecosystems, because they are long-lived compared to other organisms, and because their bodies contain recalcitrant tissues like bones and scales, it has been suggested that fish can act as a nutrient sink in pelagic freshwaters (Sereda et al., 2008).

The main ways in which a fish population can be a nutrient sink are 1) if its biomass increases, i.e., when growth and reproduction exceed mortality, 2) if emigration from the ecosystem exceeds immigration to that ecosystem, and 3) if nutrients stored in carcasses are not mineralized back to the water column, but rather remain stored in sediments in a recalcitrant form for a long time (Vanni et al., 2013). Therefore, the role of fish as a source or sink of nutrients may depend on the population dynamics, relative proportion between different life stages and conditions that control the decomposition of the carcasses (e.g. temperature).

Table 1 –Examples of internal and external processes related to nutrient cycling in freshwaters.

Process	**References**
Internal Processes	
*Animal – translocation, recycling (e.g via excretion, consumption, decomposition)	(Atkinson et al., 2017; Beasley et al., 2012; Schaus et al., 1997; Sereda et al., 2008; Subalusky et al., 2017; Vanni, 2002; Vanni et al., 2013; Williamson et al., 2018)
Re-suspension of sediments by wind and bioturbation	(Adamek and Maesalek, 2013; Boqiang et al., 2004; Forsberg, 1989; Kristensen et al., 1992; Matsuzaki et al., 2007; Sondergaard et al., 1992)
External Processes	
*Nutrient runoff from watershed	(Carpenter *et al.*, 1998; Jeppesen *et al.*, 1999; Ometo *et al.*, 2000; Vanni *et al.*, 2011; Nielsen *et al.*, 2012; Knoll *et al.*, 2015; Bucak *et al.*, 2018)
Atmospheric deposition	(Bergstrom et al., 2005; Elser et al., 2009; Jassby et al., 1994)
Transport of nutrients by migration	(Mitchell and Lamberti, 2005; Naiman et al., 2002; Vanni, 2002)

*Processes that are focused on this thesis

Therefore, from the above, the main objectives of this thesis were; (1) to evaluate, through a large scale spatial assessment, the effects that different aspects of land use and landscape properties (e.g. lake and catchment morphometry) have on biotic and abiotic properties of tropical lakes and reservoirs and whether and how such effects can be interactively dependent among each other and with precipitation; and (2) to understand through a large-scale temporal approach, whether and how an omnivorous fish is a source or sink of nutrients through its long-term population dynamics, nutrient excretion and carcass decomposition in a temperate eutrophic reservoir. In order to do that, this thesis was structured in three chapters. The specific goals pertaining to each chapter are presented below.

- ***Chapter 1*** **- Precipitation, landscape properties and land use interactively affect water quality of tropical freshwaters** - The aim of this study is to evaluate the effects of landscape properties (morphometric measurements of lakes and their catchments), precipitation patterns and land use properties (extent and proximity of the land use to water bodies) on water quality of 98 natural and artificial lakes in northeast Brazil.
- ***Chapter 2*** - **Phytoplankton community composition and structure differs among tropical lakes and reservoirs** – The goal of this chapter is to characterize lakes and reservoirs regarding the landscape properties of their surrounding areas (i.e. catchment size and catchment land use absolute and relative extent), their morphometry (i.e. ecosystem size, lake perimeter to lake volume ratio - LP:LV, and catchment area to lake volume ratio – CA:LV) and their physico/chemical characteristics, and verify whether those factors can be associated with average patterns of phytoplankton community structure at both local and regional scales across 98 lakes and reservoirs in Northeast Brazil.

- *Chapter 3* - **Fish, including their carcasses, are net nutrient sources to the water column of a eutrophic lake** - In this paper, our goal is to assess whether a fish population with high biomass and growth rate is a source or sink of nitrogen and phosphorus to the pelagic zone of a eutrophic lake, at various time scales ranging from days to 20 years.

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Chapter 1

Precipitation, landscape properties and land use interactively affect water quality of tropical freshwaters

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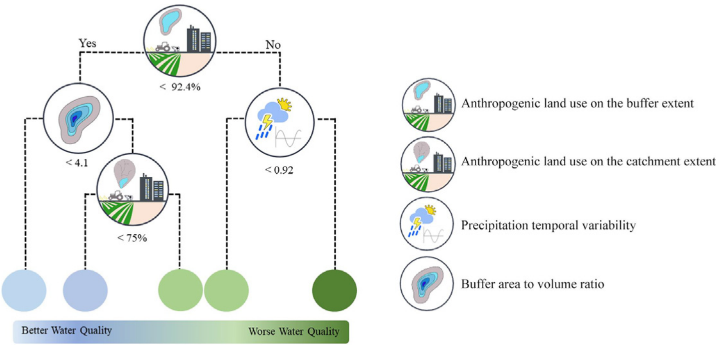
HIGHLIGHTS

- Landscape features and precipitation can mediate land use effects on water quality.
- Human land use near shores of lakes and reservoirs decreases their water quality.
- Precipitation patterns mediate the effects of land use on water quality.
- Climate and geomorphology of lakes are needed to understand land use effects.
- Effective policies for climate change and land use are vital to protect freshwater.

GRAPHICAL ABSTRACT



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ABSTRACT

Globally, conversion of pristine areas to anthropogenic landscapes is one of the main causes of ecosystem service losses. Land uses associated with urbanization and farming can be major sources of pollution to freshwaters promoting artificial inputs of several elements, leading to impaired water quality. However, how the effects of land use on freshwater quality are contingent on properties of the local landscape and climate is still poorly understood. The aim of this study was to evaluate the effects of landscape properties (morphometric measurements of lakes and their catchments), precipitation patterns, and land use properties (extent and proximity of the land use to freshwaters) on water quality of 98 natural lakes and reservoirs in northeast Brazil. Water quality impairment (WQI) was expressed as a composite variable incorporating parameters correlated with eutrophication including nitrogen (N), phosphorus (P) and Chlorophyll-a concentration. Regression tree analysis showed that WQI is mainly related to highly impacted "buffer areas". However, the effects of land use in these adjacent lands were contingent on precipitation variability for 13% of waterbodies and on surface area of the buffer in relation to the volume of waterbody (BA:Vol) for 87% of waterbodies. Overall, effects on WQI originating from the

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land use in the adjacent portion of the lake were amplified by high precipitation variability for ecosystems with highly impacted buffer areas and by high BA:Vol for ecosystems with less impacted buffer areas, indicating that ecosystems subjected to intense episodic rainfall events (e.g. storms) and higher buffer areas relative to aquatic ecosystem size (i.e. small waterbodies) are more susceptible to impacts of land use. Land use at the catchment scale was important for the largest ecosystems. Thus, our findings point toward the need for considering a holistic approach to managing water quality, which includes watershed management within the context of climate change.

1. Introduction

With the increasing human demand for natural resources caused by population and economic growth, Earth has experienced large scale transformations of its natural landscapes (Vitousek et al., 1997; Seto et al., 2012; Song et al., 2018; Marques et al., 2019). Indeed, human activities have modified a considerable proportion of natural ecosystems, for instance, farming lands, i.e. croplands and pastures (for livestock production), which occupy a combined area of approximately 34% of the Earth's ice free land surface (Ramankutty et al. 2008; Carpenter, Stanley and Vander Zanden, 2011). These changes have led to dramatic changes to the integrity of ecosystems, including their biodiversity and the maintenance of ecological functions and services they provide (Foley et al., 2005; IPBES, 2018). Freshwater systems are extremely valuable (Wilson and Carpenter, 1999), providing many ecosystem services such as human and animal water consumption, biodiversity maintenance, biogeochemical cycles, carbon storage, hydrological regulation, irrigation, fishing and recreation (Brasil et al., 2016; Carpenter et al., 1998; Daily et al., 1997; Schallenberg et al., 2013; Schindler, 2012). Although lakes, reservoirs, and rivers cover a combined area of only 2.3% of the inland surface, these ecosystems host at least 9.5% of the Earth's described animal species (Reid et al., 2019). However, they are among the most threatened ecosystems in the world (Dudgeon et al., 2006; Sala et al., 2000), experiencing higher rates of environmental degradation and biodiversity loss compared to marine and terrestrial ecosystems (Reid et al., 2019). Most threats are directly or indirectly associated with anthropogenic-mediated land use changes in their catchments (Doubek et al., 2015; Jeppesen et al., 1999; Tromboni et al., 2019; Wang et al., 2008). Indeed, the downhill position of inland aquatic systems relative to their catchments facilitates the flux of allochthonous materials toward them by gravity (Vanni et al., 2005). Therefore, anthropogenic activities occurring in catchments are major sources of nonpoint pollution to freshwaters including enhanced inputs of several chemicals, such as nitrogen (N) and phosphorus (P) (Bennett et al., 2001; Paul and Meyer, 2008; Vanni et al., 2011).

Land use-mediated nutrient inputs are brought to water bodies via surface runoff, erosion and/or leaching (Foley et al., 2005). Anthropogenic land use effects may promote cultural eutrophication and algal growth, thereby reducing water quality (Carpenter et al., 1998) and affecting ecosystem-level processes (e.g. lake productivity and nutrient cycling) and biodiversity (e.g. species richness, abundance and composition) (Cabral et al., 2019; Doubek et al., 2015; Mantzouki et al., 2015; Schindler, 2006). It can also modify the physical conditions of the aquatic environment, such as water temperature (LeBlanc et al., 1997) inorganic turbidity and water transparency (Declerck et al., 2006). In contrast, catchments with large proportions of land covered by forested areas and natural vegetation generally export lower amounts of dissolved and particulate allochthonous materials to water bodies. This buffer effect is achieved through mechanisms such as plant nutrient uptake, reduced surface runoff and reduced soil erosion (Foley et al., 2005; Lowrance et al., 1997; Mayer et al., 2007).

Several factors related to catchment land use can affect water quality, including the type of land use (i.e. croplands, pasture, urbanization) (Tang et al., 2005; Vanni et al., 2001), its extent (i.e. the area of the catchment impacted) and its proximity to the aquatic system (Declerck et al., 2006; Nielsen et al., 2012; Soininen and Luoto, 2012). For example, intensive agriculture can pollute aquatic ecosystems by the transport of fine sediments, fertilizers, and pesticides (Feld et al., 2016a; Knoll et al., 2003). Extensive livestock production on pastures promotes soil compaction, changes in vegetation cover and produces manure, with consequences for soil biogeochemical cycles, as well as the links between soil processes and the concentrations of dissolved and particulate materials in aquatic systems (Neill et al., 2001). Finally, urbanization is especially detrimental to water quality where wastewater treatment is deficient (Foley et al., 2005) and impervious surfaces are common (Hobbie et al., 2017). However, it is not clear how water quality indicators may interactively depend on other factors such as the proximity of land use to the water body (Declerck et al., 2006; Nielsen et al., 2012; Soininen and Luoto, 2012), geomorphological and topographic characteristics of catchments, morphological aspects of the aquatic system itself, and climate (Alahuhta et al., 2011; Hayes et al., 2015; Mattsson et al., 2005; Price, 2011). For instance, even if most of the catchment is anthropogenically impacted, it is possible that more pristine land cover in the portions adjacent to the lake could still buffer the impact of nutrients and sediment transport to the water body (Carpenter et al., 1998; Dodson et al., 2005; Muscutt et al., 1992). On the other hand, water quality can be severely affected by land use impacts concentrated in regions adjacent to the water body (Tran et al., 2010).

Landscape properties such as soil type, topography (e.g. slope), the absolute and relative size of catchments and their aquatic systems (Bremigan et al., 2008; Hayes et al., 2015; Vannote et al., 1980) and the origin (i.e. natural or artificial) of the aquatic systems (Dodson et al., 2006; Nielsen et al., 2012) are factors that affect the magnitude of transport rates of allochthonous material to waterbodies, as well as determine the sensitivity of these systems to external inputs of materials. Therefore, landscape properties can also mediate, through complex ways, the effects of land use properties on aquatic systems. Finally, the magnitude and variability of precipitation can either intensify (e.g. via soil percolation or surface runoff) or attenuate (e.g. via dilution) land use effects on aquatic systems (Jeppesen et al., 2015).

Combined long-term monitoring data for water quality and catchment land use dynamics are scarce (but see, e.g. Renwick et al., 2008, 2018; Richards et al., 2009), but an alternative approach to understanding the complexity of interactions among the aforementioned mechanisms is to use a space-for-time approach comprising aquatic systems that are distributed over large spatial scales (Soranno et al., 2017, 2019). The main goal of this study is to evaluate whether and how landscape properties and precipitation mediate the effects of land use properties on tropical inland aquatic systems in northeast Brazil. For this, we sampled 98 aquatic ecosystems distributed over 29,000 km^2 encompassing different origins (i.e. natural lakes and human-made reservoirs), climate (i.e. humid and semi-arid), landscape properties (i.e. the absolute and relative morphometric measurements of lakes, reservoirs and their catchments), and land use patterns (i.e. extent and proximity of land cover to the water body) (Cabral et al., 2019; Junger et al., 2019). This study has the potential to provide essential information for decision making regarding land management and freshwater conservation.

2. Methods

2.1. Study area

This study was performed during the dry season of 2012 (September) across 98 lentic water bodies located in the state of Rio Grande do Norte, northeastern Brazil (Fig. 1). These environments encompass perennial natural lakes ($n = 30$) and man-made artificial reservoirs ($n = 68$) formed by dams constructed between 1915 and 1950 by the National Department of Works for Drought Control (DNOCS, 2015). Their location ranges from the coastal to the semi-arid region, encompassing 14 (out of 16) watersheds of the state. Sixty-eight percent of the studied ecosystems are located in a semi-arid region (annual precipitation ≈ 400–800 mm) with the remaining ecosystems distributed along the coastal region within a sub-humid and humid climate (annual precipitation ≈ 800–1200 mm) (BSh climate, Köppen classification). Most systems are shallow (90% with depth < 4 m) and have small surface area (89% < 1 km^2) (Table 1). The majority of ecosystems in the semi-arid region are artificial reservoirs (85%), while reservoirs and natural lakes encompass 35% and 65% of aquatic systems distributed across the coastal humid climate, respectively (Fig. 1). The spatial distribution of studied aquatic systems spans a gradient of catchment land use and trophic state, ranging mostly from pristine forested areas to agricultural land cover and from oligotrophic to hyper-eutrophic conditions (Table 1) (Cabral et al., 2019; Junger et al., 2019).

2.2. Field sampling and determination of the water quality parameters

Impaired water quality is commonly associated with cultural eutrophication, caused by the excessive inputs of N and P (Carpenter et al., 1998). Phytoplanktonic chlorophyll-a (Chl-*a*) has also been considered a proxy for productivity and trophic state of waterbodies (Boyer et al., 2009). Therefore, we used concentrations of N, P and Chl-*a* as proxies for water quality. To obtain concentrations of N, P and Chl-*a* for each lake, water samples were collected from the subsurface portion (approximately 0.3 m deep) of the water column with a Van Dorn sampler. Samplings were performed at six sites in littoral and limnetic habitats (3 per habitat) and integrated into a single sample per water body. Water samples were analyzed in the laboratory for Chl-*a*, total nitrogen (TN) and total phosphorus (TP) (Valderrama, 1981). Determination of TN (mg L^{-1}) was done by a carbon analyzer (TOC-V) coupled with a nitrogen analyzer (VPN module) and an autosampler (Shimadzu). Total phosphorus (mg L^{-1}) was determined by persulfate oxidation followed by measurement of reactive soluble phosphorus method (Murphy and Riley, 1962). Determination of Chl-*a* (μg L^{-1}) was made according to (Jespersen and Christoffersen, 1987)

Because TP, TN, and Chl-*a* were all significantly correlated with each other (Table 2), and for better interpretability, we created a "water quality impairment" composite variable (hereafter, water quality impairment, WQI) by running a Principal Component Analysis (PCA) on the three response variables, (similarly to Knoll et al., 2015). We performed a broken-stick distribution to evaluate how many PCA axes were significant.

2.3. Measurements of precipitation, landscape, and land use properties

Lake morphometric characteristics, i.e. surface area and perimeter, were calculated through satellite image processing (delineation of polygon shapefiles) using ArcGIS 10.5 (ESRI, 2017). Lake depth was measured at the central part of each lake using a calibrated rope, and lake volume was calculated through the hyperbolic function 0.43 × lake area × depth (Post et al., 2000). To analyze the importance of spatial scale (distance between the lake and the respective land use) on the effects of land use on water quality, total catchment areas and buffer areas, were delineated for each lake. It is relevant to note that buffer areas in the context of this study depicts the near-freshwater land zone around the water body comprising a distance of 100-meter from its shore, differently from the more classic use of the term "buffer zones" which defines a portion of permanently conserved natural vegetation along a watercourse (Karr and Schlosser, 1978; Muscutt et al., 1992). Delineation of catchments were based on lakes polygon shapefiles and it was performed using ArcHydro 2.0 Toolbox (Arc Hydro Tools, 2011) on ArcGIS 10.5 (ESRI, 2017). Details on methodology for catchment area delineation can be found on supplementary material.

To avoid mismatches between the catchment area and buffer area, buffers were manually edited to fit within the catchment area of their specific lake. Morphometric landscape properties (catchment and buffer area) were calculated in ArcMap 10.5 (ESRI, 2017). Morphometric characteristics as the catchment area-to-lake volume ratio (CA:Vol), buffer area-to-lake volume ratio (BA:Vol) and lake perimeter-to-lake volume ratio (LP:Vol) were also calculated as they are expected to influence the connectivity on the land-water interface (Table 3).

Slope (an indicator of steepness) of catchment and buffer area was also measured for each lake. We extracted slopes from a 30-m digital elevation model (DEM) comprising the state of Rio Grande do Norte using the slope function at ARCMAP software. Data was gathered from the Brazilian Geomorphometric database (TOPODATA), available at http://www.dsr.inpe.br/topodata/acesso.php. However, because the region studied is mostly flat, average slope of all catchments and buffers did not present a lot of variation (mean and SD; 2.1° ± 1.24°; 1.97° ± 0.77°, respectively) so we decided to not include this variable in further analysis.

Land use proportions relative to the year of 2012 were quantified for each catchment area and buffer area using data available through Project MapBiomas - Collection 3 of Brazilian Land Cover & Use Map Series (Projeto MapBiomas, 2018). Total area of each land use type was calculated on ArcGIS 10.5. Subsequently, categories of land use provided by MapBiomas were grouped within two main groups: forested areas and anthropogenic areas. Anthropogenic use includes urban/developed zones and agriculture areas (cropland and pasture). They were grouped as these types of land use are expected to have similar effects on the increase of nutrient inputs on waterbodies (Foley et al., 2005). As forest land cover and anthropogenic land cover were strongly negatively correlated, we used only anthropogenic land use in the model.

To address the temporal variability in precipitation present in the dataset, the magnitude and temporal variability of precipitation (hereafter, Tot_{precip} and Cv_{precip}, respectively) for each lake were computed. There are seven weather stations distributed across the state of RN and for each one of them, the magnitude of precipitation was calculated as total monthly cumulative precipitation from September 2010 to September 2012 (Source: INMET – Instituto Nacional de Meteorologia). To estimate precipitation temporal variability, the coefficient of variation was obtained from monthly cumulative precipitation data for the same period. To obtain the magnitude and the temporal variability of precipitation for each lake, the weighted average of the values for the different stations was computed, with weights proportional to the distance between the lake and the stations. Values obtained with the interpolation approach are consistent with spatial variability in precipitation expected by the Worldclim long-term (1970–2010) (Fick and Hijmans, 2017; Fig. S2). More details about how the precipitation was computed can be found on the supplementary material.

2.4. Statistical analysis

We used a regression tree analysis (RTA) to verify how water quality impairment is related to precipitation, landscape, and land use properties. RTA is a non-parametric statistical technique that allows one to explain the variation of a single response variable by one or more explanatory variables (Breiman et al., 1984; DE'ath and Fabricius, 2000). Advantage of RTA over other multivariate tests is that it can unravel interactions among predictors and produces a straightforward

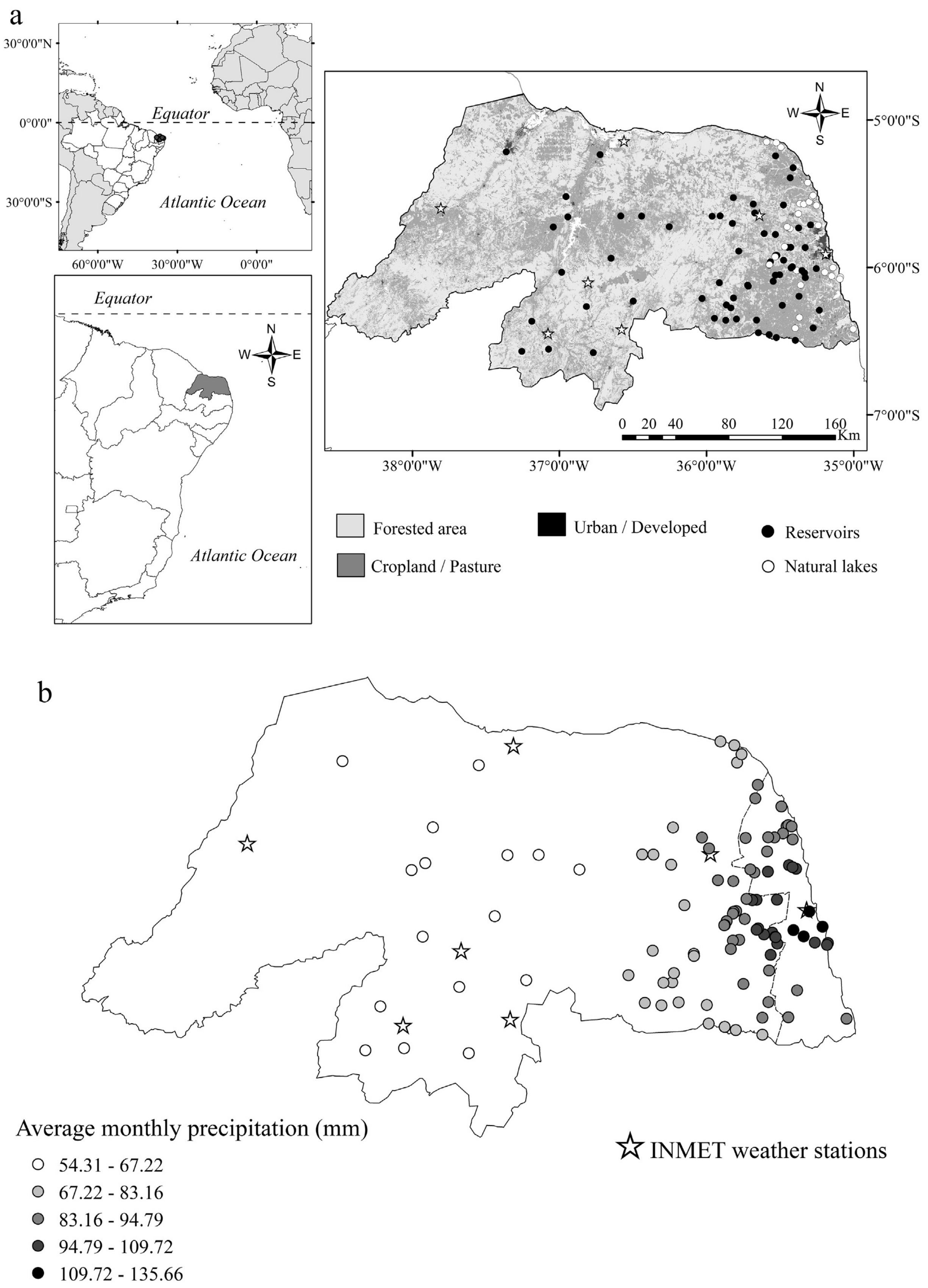

Fig. 1. Panel *a* show the studied lakes sampled on Rio Grande do Norte, Brazil. Natural lakes are represented by white dots and reservoirs by black dots. Land cover types were grouped according to the purposes of this study. Natural vegetated areas refers to natual forest, savanna and grassland formations. Anthropogenic land use encompasses farming (agriculture/pasture) and urban land uses. Original data was available through Project MapBiomas - Collection 3 of Brazilian Land Cover & Use Map Series. Map was build using ArcGIS 10.5.1 (ESRI, 2017). Panel *b* is presenting the average monthly precipitation from 2010 to 2012 in the studied lakes calculated from interpolation of the seven INMET automatic weather stations (stars). The dashed line depicts the semi-arid delimitation according to SUDENE, 2017. To the right of the line is the humid region and to the left is the semi-arid.

Table 1
Overview of landscape and land use general properties (mean ± SD & range) for lakes studied. Anthropogenic land use was composed by the combination of agriculture/pasture and urban/developed land uses, which are complementary to the forested/vegetated land use. CA depicts catchment area.

Variables	Mean	±SD	Max	Min
Landscape properties				
Lake area (km^2)	0.77	2.05	13.29	0.00
Lake perimeter (m)	5271.54	10,003.24	54,448.19	219.18
Lake depth (m)	1.91	1.11	4.50	0.20
Lake volume (m^3)	844,689.26	2,565,547.18	17,878,648.09	1372.14
Catchment area (km^2)	128.46	371.42	2043.20	0.07
Buffer area (km^2)	0.48	0.87	4.77	0.03
Buffer perimeter (m)	10,030.02	17,664.04	96,291.73	811.00
Land use properties				
%Forested (CA)	37	26	100	0
%Forested (buffer)	37	27	100	0
%Anthropogenic (CA)	62	26	99	1
% Agriculture/Pasture	60	25	100	0
% urban/developed	3	7	48	0
%Anthropogenic (buffer)	60	27	99	1
% Agriculture/Pasture	55	27	100	0
% urban/developed	5	10	58	0

way to graphically visualize these interactions. When carrying out regression tree analysis, it is necessary to control the number of explanatory variables entering the model to avoid overfitting of the data. As a rule of thumb, the number of samples should be around one order of magnitude larger than the number of variables (Harrell, 2001; Feld et al., 2016b). Hence, given that we have 98 samples, initially we choose seven explanatory variables that were related to water quality in previous studies (the rationale for including these parameters on the model can be found in Table 3). These variables are: precipitation magnitude (Tot$_{precip}$), precipitation temporal variability (CV$_{precip}$), proportion of anthropogenic land use in the catchment area and in the buffer extent (Ant$_{CA}$ and Ant$_{BA}$), lake perimeter to volume ratio, and catchment area and buffer area to volume ratios (CA:Vol and BA:Vol). Then, we further conducted a selection of variables to exclude the ones that presented high levels of correlation and/or a high variance inflation factor (VIF > 8; Feld et al., 2016b). Correlation and VIF analysis were conducted with R using the stats (R Core Team, 2017) and usdm (Naimi et al., 2014) packages, respectively. Pairs of variables which are expected to have similar ecological interpretation (i.e.Tot$_{precip}$ and cv$_{precip}$; LP:Vol and BA:Vol) presented high correlation and similar high VIF values (Tables 1 and S2). For this reason, we choose only one variable from each highly correlated pair to enter in the model. Because the close values from the VIF analysis do not allow us to choose the best variable to be kept in the model (Table S2), we ran four alternative models using pairwise combination of these variables to select the best fit model (See Table 4).

RTAs were performed using the rpart package in R (Therneau et al., 2017). The regression tree was built by considering the optimization of two main hyperparameters: the minimum number of splits (minsplit) and the complexity parameter (cp). For machine learning standards, the size of our dataset ($n = 98$) is rather small and for this reason, we choose to apply leave-one-out cross validation (LOOCV) to choose both, minsplit and cp. This way, we can ensure that the chosen minsplit-cp pairs the one that generalizes better for the kind of lakes studied. A more detailed version of the RTA analysis performed can be found in the supplementary material. In the result section, we report the R^2 (R^2 = 1 – relative error) which represents the percentage of variation in the dataset explained by our model and the RMSE, the square root of the variance of the residuals, which indicates the absolute fit of the model. Lower values of RMSE represent a better fit. For statistical purposes of normality improvement, proportions of anthropogenic land use and the coefficient of variation of precipitation (CV$_{precip}$) were logit transformed, log(p/[1-p]) (Warton and Hui, 2011). All other variables were $\log_{10}(x + 1)$ transformed.

3. Results

The first principal component (PC1 or WQI) of the PCA analysis for water quality indicators (TN, TP, and Chl-*a*), explained 66% of the variance among the studied freshwater systems (Fig. 2) and it was positively and significantly correlated with TP (Pearson correlation $r = 0.79$), TN ($r = 0.79$) and Chl-*a* ($r = 0.86$) (Table 2). Hence, the WQI represents well the water quality parameters considered. Additionally, only the first dimension of the PCA presented a larger percentage of accumulated variance than the broken-stick variance (Table S1), thus the scores of the first axis were used as our WQI composite variable (Legendre and Legendre, 1998). The scores of PC1 denote a WQI value for each individual lake and it ranged from −1.69 to 5.60. Higher values of the WQI are related to higher concentrations of TN, TP and Chl-*a*, representing lakes with higher trophic status and worsen water quality, while lower values reflect lower concentrations of these parameters and thus relatively better water quality.

The best fit model (Table 4) from the RTA included the following explanatory variables: CV$_{precip}$, Ant$_{CA}$, Ant$_{BA}$, CA:Vol and BA:Vol. From the total of the five possible predictors that entered in the final RTA, four were selected by the regression tree model: CV$_{precip}$, Ant$_{CA}$, Ant$_{BA}$, BA:Vol (Fig. 3). This model explained 42% of the variance (R^2 = 1 – relative error) of the WQI within the dataset. According to this model, decreased water quality is associated with highly anthropogenic land use (Ant$_{BA}$ > 92%) near the shores of lakes and reservoirs (within the 100 m buffer area). This first split alone explained 24% of the variance in the model. The negative effect of Ant$_{BA}$ on water quality is intensified by its interaction with precipitation, as areas with high variability in precipitation showed higher WQI (WQI = 3; right side of the tree). Lakes with <92% of the anthropogenic area within the buffer, but with higher BA:VOL, and >75% of anthropogenic use in their catchment, showed relatively high values of WQI. At this point in the tree, it is

Table 2
Correlation matrix among the main variables studied. Significant correlations (Pearson correlation, $p \le .05$) are highlighted in bold. Non-significant correlations are in light grey.

Variables	TP	TN	Chl-*a*	WQI	Tot$_{precip}$	CV$_{precip}$	LP:VOL	CA:VOL	BA:VOL	Ant$_{CA}$
TN	0.40									
Chl-*a*	**0.54**	**0.49**								
WQI	**0.78**	**0.75**	**0.86**							
Tot$_{precip}$	**−0.49**	−0.16	−0.16	−0.29						
CV$_{precip}$	**0.50**	0.11	0.18	0.3	**−0.86**					
LP:VOL	0.45	0.22	0.18	0.34	−0.16	0.17				
CA:VOL	0.30	0.22	0.09	0.23	−0.3	0.24	**0.53**			
BA:VOL	0.47	0.26	0.26	0.4	−0.08	0.15	**0.93**	**0.48**		
Ant$_{CA}$	0.19	0.21	0.36	0.35	0.23	−0.12	0.13	**−0.23**	0.2	
Ant$_{BA}$	0.35	0.23	0.31	0.4	−0.18	0.29	0.05	−0.15	0.11	**0.53**

TN: total nitrogen; TP: total phosphorus; Chl-*a* = chlorophyll – *a* concentration; Tot$_{precip}$: magnitude of precipitation; CV$_{precip}$: temporal variability of precipitation; LP:Vol: lake perimenter to lake volume ratio; CA:Vol: catchment area to lake volume ratio; BA:Vol: buffer area to lake volume ratio; Ant$_{CA}$: proportion of anthropogenic land use on the catchment area; Ant$_{BA}$: proportion of anthropogenic land use on the buffer area.

Table 3
Description of variables used in the Regression Tree Analysis model.

Variables	Units	Rationale	Source	Measurement method	Mean ± SD, (min, max)
Response variable					
Total nitrogen (TN)[a]	mg L^{-1}	Important limiting nutrient for autotrophic and heterotrophic production in freshwater ecosystems (Elser et al., 1990).	Our survey	Total Carbon Analyzer coupled with the TN analyzer module (TOC-VPN;Shimadzu).	4.91 ± 2.27 (0.91, 13.18)
Total phosphorus (TP)[a]	mg L^{-1}	Important limiting nutrient for autotrophic and heterotrophic production in freshwater ecosystems (Elser et al., 1990).	Our survey	After oxidation of organic phosphate compounds using persulfate (Valderrama, 1981) and measured by the soluble P method (Murphy and Riley, 1962).	0.23 ± 0.20 (0.02, 1.04)
Chlorophyll-*a* (Chl-*a*)[a]	μg L^{-1}	Proxy of phytoplankton primary production which may increase light attenuation and turbidity. (Boyer et al., 2009, Williamson et al., 2018)	Our survey	Pigments extracted from filters with 95% ethanol and absorbance measured at wavelengths 665 and 750 nm (Jespersen and Christoffersen, 1987).	62.62 ± 115.21 (0.334, 628.30)
Water quality impairment (WQI)		Proxy of water quality.	Our survey and R version 1.1.442	The water quality impairment index (WQI) was obtained through a Principal Component Analysis (PCA) of water quality related variables (TN, TP and Chl-*a*). PCA was performed in R v 1.1.442 using the Vegan package.	0.00 ± 1.4 (−1.69, 5.60)
Explanatory variables					
Landscape Properties					
Lake perimeter to volume ratio (LP:Vol)		Represents the potential magnitude of connectivity, by volume unit, between the aquatic system and the adjacent terrestrial ecosystem. Higher ratios are expected to relate with higher input of nutrients. (Hakanson, 2004)	Our survey and TOPODATA	Lakes polygon shapefiles (ArcGis 10.5.1 - ESRI, 2017) to obtain area and perimeter, field survey to obtain lake depth. Lake volume as calculated from the hyperbolic function 0.43 × Lake area × Depth (Post et al., 2000)	0.04 ± 0.05 (0.003, 0.24)
Catchment area to lake volume ratio (CA:Vol)		Represents the potential magnitude of allochthonous inputs, by volume unit, derived from the aquatic ecosystem catchment area. Can also represent a water renewal ratio for some in-lake processes. Higher ratios are usually related to higher concentrations of nutrients and lower water transparency. (Thornton 1990, Timms, 2009; Nõges, 2009, Knoll et al., 2015)	Our survey and TOPODATA	Lakes and lake catchments polygon shapefiles (ArcHydro 2.0 Toolbox - ArcHydro, 2011 - on ArcGis 10.5.1 - ESRI, 2017). Volume was calculated as mentioned above.	618.25 ± 2422.95 (0.75, 21,004)
Buffer are to lake volume ratio (BA:Vol)		Represents the potential magnitude of allochthonous inputs, by volume unit, derived from the proximal zone of the aquatic ecosystem. Higher ratios are usually related to higher concentrations of nutrients and lower water transparency. (Thornton 1990, Nõges, 2009)	Our survey and TOPODATA	Lakes and buffer areas polygon shapefiles (ArcGis 10.5.1 - ESRI, 2017). Volume was calculated as mentioned above.	4.58 ± 6.42 (0.26, 30.68)
Precipitation characteristics					
Total precipitation	mm	Represents the potential amount of nutrients and matter entering the aquatic ecosystems due to runoff of allochthonous material via subsurface and groundwater flow. May also increase the volume of lakes causing the dilution of nutrients. (Hayes et al., 2015)	INMET	Monthly cumulative precipitation from September 2010 to September 2012.	2116 ± 392 (1344, 3388)
Precipitation temporal variability	%	Represents the variability on the potential amount of nutrients and matter entering the aquatic ecosystems due to runoff of allochthonous material via subsurface and groundwater flow. (Hayes et al., 2015)	INMET	Coefficient of variation obtained from monthly cumulative precipitation data from September 2010 to September 2012	1.17 ± 0.09 (0.95, 1.41)
Land use properties					
Anthropogenic area	%	Represents the magnitude and quality of allochthonous material entering aquatic ecosystems. It considers the type of land use, proximity of use (buffer or catchment area) and extension of land use (total area of catchment and buffer). Has the potential to increase nutrient inputs to inland waters, leading to eutrophication and decreased water quality (Carpenter et al., 1998; Knoll et al., 2015)	Mapbiomas 3.0	Land use classification for Caatinga and Atlantic Forest biomes. Agriculture, pasture and urban/developed uses were grouped into Anthropogenic use (Ant) as these types of land use usually have similar effects on the increase of allochthonous nutrient inputs to waterbodies (Foley et al., 2005).	Buffer (Ant_{BA}): 60 ± 27 (0.1, 99) Catchment (Ant_{CA}): 62 ± 26 (0.1, 99)

Adapted from Junger et al., 2019

[a] TN, TP and Chl-*a* were combined into a Water quality impairment index (WQI) to be entered as the response variable in the model.

worth noting the difference on the WQI generated by the Ant_{CA} split. While lakes with the same other conditions, but with higher percentages of Ant_{CA} (>75%) had a WQI of 1.5, lakes with less impacted catchments presented much lower values of water quality impairment. The lowest values of WQI (−0.51, left side of the tree), thus lower concentration of nutrients and Chl-*a*, were related to lower percentages of anthropogenic land use in the buffer and lower buffer area to volume ratio. BA:Vol explained an additional 8% of the WQI variance within the dataset.

4. Discussion

Although it is well known that water quality is impaired by external inputs of nutrients derived from anthropogenic land use (Baker, 2003; Carpenter et al., 1998; Nielsen et al., 2012; Vanni et al., 2011), our study shows that the effects of land use on water quality are modulated by a combination of precipitation patterns and landscape properties. This finding reinforces the importance of inclunding potentially interactive environmental variables (e.g. hydromorphological variables) when

Table 4
Alternative RTA Models ran with pairwise combination of Tot_{precip} & CV_{precip} and LP:Vol & BA:Vol to select the best fit model. The model that presented the combination of higher R^2 and lowest RMSE was chosen as the best fit model (highlighted in bold).

Alternative RTA models	R^2	RMSE
WQI ~ CV_{precip} + CA:Vol + BA:Vol + Ant_{BA} + Ant_{CA}	**0.42**	**1.40**
WQI ~ Tot_{precip} + CA:Vol + BA:Vol + Ant_{BA} + Ant_{CA}	0.24	1.45
WQI ~ Tot_{precip} + CA:Vol + LP:Vol + Ant_{BA} + Ant_{CA}	0.38	1.43
WQI ~ CV_{precip} + CA:Vol + LP:Vol + Ant_{BA} + Ant_{CA}	0.38	1.43

WQI: water quality impairment; Tot_{precip}: magnitude of precipitation; CV_{precip}: temporal variability of precipitation; LP:Vol: lake perimenter to lake volume ratio; CA:Vol: catchment area to lake volume ratio; BA:Vol: buffer area to lake volume ratio; Ant_{CA}: proportion of anthropogenic land use on the catchment area; Ant_{BA}: proportion of anthropogenic land use on the buffer area.

acessing the impacts of land use on water quality (Leigh et al., 2010). Overall, our results indicated that these interactions are more relevant for water bodies located in the semi-arid region and for small and shallow lakes and reservoirs. Ecosystems subject to higher variability in the precipitation regime (e.g. intense sporadic rainy events interspersed with drier periods) and larger buffer areas relative to aquatic ecosystem size (i.e. shallow and/or small waterbodies) are more susceptible to the impacts of land use on near-freshwater land zones. Here we discuss the different terrestrial-aquatic interaction mechanisms that affect the water quality of the studied ecosystems, and implications of these results.

4.1. Land use

The 98 studied lakes showed high variability in landscape and land use properties (Tables 1 and 3). On average, anthropogenic land use comprised over 60% of both catchment and buffer areas, and it was mainly dominated by cropland and pasture land cover. It is worth noting that cropland and pasture in this study area mostly consists of subsistence family farmers, fruticulture and sugar cane crops (Aquino and Lacerda, 2015).

The percentage of anthropogenic land use at the adjacent area of the water bodies was the main variable related to impaired water quality, which is in accordance with previous studies (Karr and Schlosser, 1978; Lowrance et al., 1997; Mattsson et al., 2005; Schindler and Fee, 1974; Tran et al., 2010). Indeed, as shown in Mayer et al. (2007) and Muscutt et al. (1992), conserved buffer strips can intercept anthropogenic pollutants, carried along surface or subsurface pathways, before they reach the aquatic ecosystem. However, land use at the catchment scale was also critical for distinguishing lakes based on water quality impairment (WQI). This result indicates that to safeguard water quality, not only the protection and conservation of nearby areas of the aquatic systems are important, but also it is fundamental to consider the land use characteristics of the whole catchment area (Fraterrigo and Downing, 2008; Knoll et al., 2015; Nielsen et al., 2012; Wang et al., 1997). This is especially relevant for small and shallow lakes. Accordingly, when studying southeastern Ontario wetlands, Houlahan and Findlay (2004) suggested that land use effects on water quality can be derived from longer distances away from lake margins. More specifically, they found that water N and P concentrations were negatively correlated with forest cover at 2250 m from the wetland edge. Additionally, Fraterrigo and Downing (2008) suggested that the ability of the catchment to convey materials to water bodies can help explain the extent to which land use affects water quality. Although we did not measure data related to catchment transport capacity, including such data in future studies could help to elucidate part of the unexplained variability in our model.

The finding that land use in the buffer area, as well as in the catchment as a whole, can modulate water quality has implications for water management that should be considered. These results contrast with commonly applied strategies of management policies that focus mainly on regulation of nutrients inputs to agricultural fields and implementation of near-water conservation buffer areas. Our findings suggest they should also incorporate strategies to reduce the proportion of farming related land uses in the catchment of water bodies (Nielsen et al., 2012). Special consideration should be given in the context of the Brazilian Forestal Code approved in 2012 (Law no. 12651/12), that updates the width of buffer areas for hydrological resources protections (Permanent Preservation Areas - PPA) ranging from 30 to 100 m according to land use, lake type (natural or artificial) and lake size (Brasil, 2012). For example, for lakes smaller than 0.2 km^2 within rural areas, the law demands a buffer area of 50 m and does not consider other characteristics of the catchment. More critically, the law no longer requires (in comparison to the former 1965 Forestal Code) a PPA buffer of any extent for artificial or natural lentic systems with <0.01 km^2 (which are the majority of lakes in semi-arid region of Brazil (Brancalion et al., 2016). Varela et al. (2019), studying the efficacy of different riparian buffer area extents to preserve water quality in a PPA located at

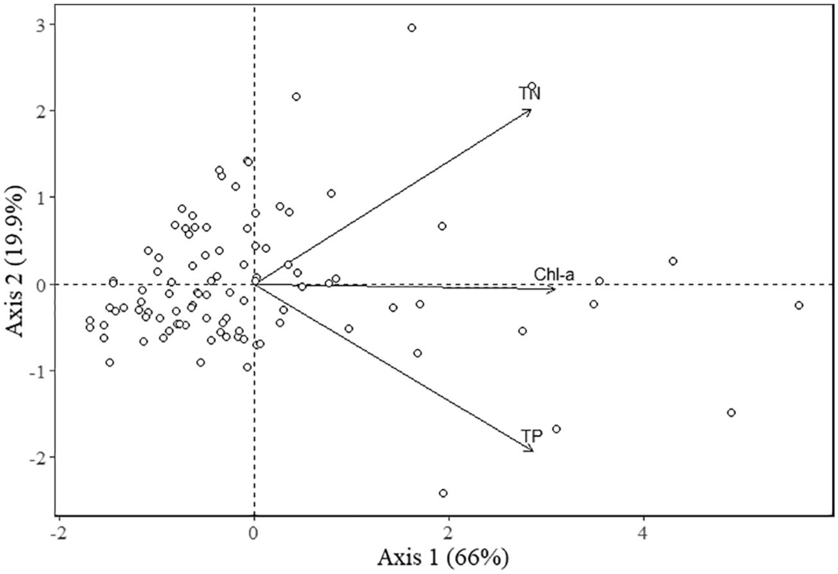

Fig. 2. PCA biplot of water quality parameters (TP, TN and Chl-*a*) from the 98 lakes studied at Rio Grande do Norte, Brazil.

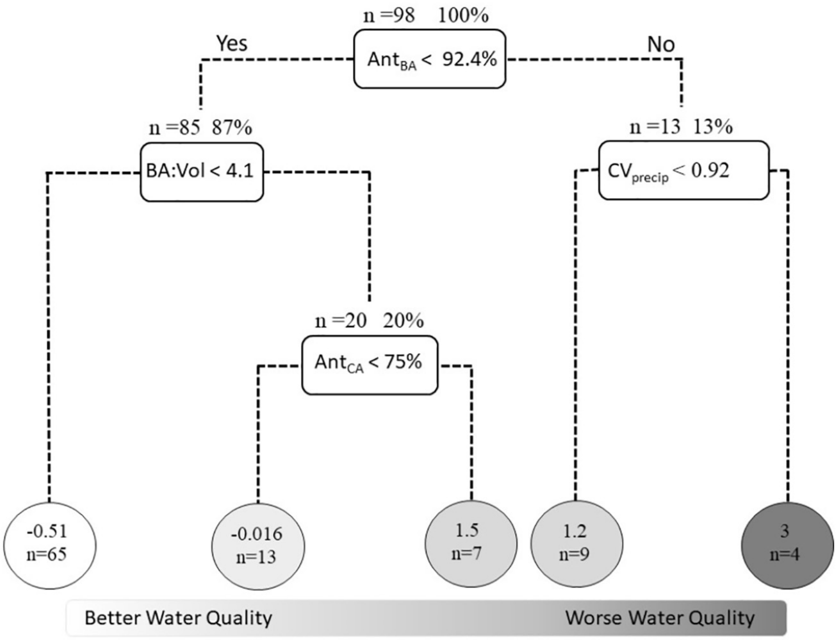

Fig. 3. Regression tree showing the relationships between water quality impairment (WQI) and precipitation, landscape and land use properties for the studied lakes. WQI is a composite response variable originated from the PCA using TN, TP and Chl-*a*. High values indicates low water quality (higher concentration of nutrients and Chl-*a*) and low values indicate less impaired water quality. Each split in the tree represents a Yes or No answer to the condition stated in each node box. Circles represents terminal nodes and it lists the mean value of the WQI and the number of lakes belonging to this group. Ant_{BA}: % of anthropogenic land use on the buffer extent; Ant_{CA}: % of anthropogenic land use on the catchment area extent, CV_{precip}: temporal variation of precipitation; BA:Vol: buffer area to volume ratio.

Minas Gerais, Brazil, found that 50 m wide riparian buffers were not enough to protect streams from having poor water quality. They suggest that the minimum area imposed by this law should be substantially enlarged. Our data highlights the benefits of the potential expansion of this law, adding the need to also regulate the proportions of land use and protected areas within the catchment area of freshwaters, as at least 25% of the preserved area on the catchment was necessary to improve water quality based on our dataset.

4.2. Landscape properties/morphometry

Our results are also in accordance with recent works showing that land use effects on water quality are best predicted when combined with complementary environmental parameters such as climatic and morphometric variables (Bucak et al., 2018; Catherine et al., 2010; Knoll et al., 2015). Knoll et al. (2015) found that elevated trophic status in Ohio-US lakes were associated with high anthropogenic land use, shallow lake depth, and high catchment-to-water surface area ratio (CA:SA). Catherine et al. (2010), studying lakes and reservoirs in France showed that concentration of Chl-*a*, a proxy of eutrophication, was explained by the interaction of multiple variables. Chl-*a* was positively correlated with increased CA:SA, high altitude, higher temperatures and higher proportions of anthropogenic land use (measured as impervious surfaces). TP concentration was positively associated with percentage of open cultivated land and the CA:SA in a study of 95 Swedish lakes (Hakanson, 2005). These studies collectively support the idea that large CA:SA is usually related to higher transportation of material from land to water. Similarly, our model suggests that the larger the buffer area proportionally to the lake volume, it is more likely that water quality will tend to decrease (higher WQI). Thus, it is highlighted here that the relationship between BA:Vol and water quality can also mean that small and shallow lakes are more susceptible to the effects of land use on water quality than lakes with proportionally greater volume and similar buffer areas.

4.3. Precipitation characteristics

In general, precipitation is expected to increase the flux of nutrients to freshwaters because of increased runoff (Carpenter et al., 2018). Meanwhile, during droughts, the runoff is reduced, potentially decreasing nutrient loading (Jeppesen et al., 2011). However, dry periods are associated with higher evaporation levels (negative water balance) and overall volume reduction in lakes and reservoirs, usually leading to enhanced concentration of nutrients and consequently, to eutrophication (Brasil et al., 2016; Jeppesen et al., 2015; Rocha-Jr et al., 2018). Short residence times (which occur during dry periods) can also promote cyanobacteria blooms (Elliott, 2010; Romo et al., 2013). In the northeast Brazil, Brasil et al. (2016) and Costa et al., (2016) found that the dry season induced reductions in lake volume and lead to increases in the nutrient concentrations, phytoplankton, and cyanobacteria biomass, compromising water quality. Despite the expected effects of precipitation on nutrient runoff, our results imply interactive effect of precipitation variability and land use on water quality impairment.

The year in which data for this study was collected (2012) was particularly well suited to analyze the impact of precipitation variability on water quality. Indeed, 2010 was a dry year in northeast of Brazil, while 2011 presented slightly above average rainfall, and it was followed by severe droughts in 2012 (Marengo et al., 2016). Hence our study lakes located in the semi-arid regions faced especially variable precipitation regimes. Our model showed that lakes experiencing relatively variable precipitation regimes have lower water quality. The effects of precipitation variability on water quality may be the combined result of both mechanisms: concentration of nutrients during the dry periods (due to volume reduction) enhanced by increased allochthonous runoff during sporadic rainy events. These, seasonal rainfall events may act as temporal “hot-moments”, representing a large input of allochthonous material into aquatic systems affecting their primary production (Sadro and Melack, 2012), even if they occur for short-term periods (Williamson et al., 2018). Additionally, because most of them receive contributions exclusively from intermittent rivers, their inflow rates are very low, contributing to increased water residence time and high nutrient concentrations that promotes eutrophic conditions (Menezes et al., 2018; They et al., 2017). The Brazilian semi-arid area has the highest population density of any dryland in the world (Marengo, 2008) and the reliance of local populations on water resources imposes a strong pressure on aquatic systems. Furthermore, this region is being affected by climate change, with predicted warmer and drier conditions in the current century (IPCC, 2014). Therefore, this is a region of critical interest, where a better understanding of the interactive effects of land use, climate, and landscape properties on water quality can diminish the conflicts between environmental impacts and water resources supply.

4.4. Caveats and future perspectives

Our models explained a good proportion of variability in our dataset ($R^2 = 42\%$), but there is still considerable unexplained variance. There are other factors that were not measured in our study that can be important to explain the concentration of water quality parameters in these freshwater systems. For instance, there are particular characteristics of the water bodies related to the type of soil (e.g texture, fertility) that can also interact with climatic characteristics affecting surface runoff and the flux of nutrients from land to water. It is relevant to note that the studied lakes located in the humid zone are dominated by natural lakes (65% of the aquatic systems). These coastal natural lakes are situated in sand dunes and in deep soils with low fertility compared to the shallow and more fertile soils of the semi-arid region (Brito, 2010). Additionally, they usually have lower CA:SA ratios than reservoirs (Junger et al., 2019;) hence, the natural coastal lakes receive potentially lower inputs of allochthonous materials from surface runoff, which also can be filtered via soil percolation before arriving at the waterbody. Moreover, the coastal natural lakes are generally supplied by groundwater (Menezes et al., 2018; Junger et al., 2019), thus the water quality in these habitats may be less influenced by precipitation variability than lakes and reservoirs located in the semi-arid region.

5. Conclusions

In summary, we conclude that effective management of water quality requires consideration of land use adjacent to lakes and the whole catchment, as well as lake morphometry and precipitation. In order to protect freshwaters, it is also of greatest importance to consider climate change scenarios. Considering the predicted scenario of warming and lower precipitation levels in the Brazilian Northeast in the near future (Marengo et al., 2016), the only way to prevent water shortages and water quality degradation is to conserve and restore the natural terrestrial ecosystems in the watersheds. According to our model, special attention should be given to small and shallow lakes and lakes with relatively high buffer area in relation to lake volume, which are located in areas with higher precipitation temporal variability and strong anthropogenic pressure in their surroundings. Being able to model and predict consequences of increased habitat alteration and effects of climate change, combined with easily obtained morphometric data of lakes, can be a helpful additional tool to integrate freshwater quality management. Future research should focus on the development of predictive models of risk assessment for lakes, and recognize the lakes that are priorities for management actions. This would optimize policies regarding land use and delineation of protected areas near waterbodies. In that way, the water quality and its multiple uses within the watersheds can be preserved.

Author statement individual contribution

AC, LSC, RLGN & CRC designed the study.

LSC get the funding.

CRC, FCA, FCCD & LBQ carried out the field work and laboratorial analysis for water parameters.

AMA provided reagents and laboratorial infrastructure to conduct water nutrient analysis.

RLGN, EMV, FCA, JG conducted the methods to obtain land use and landscape data used in the study.

RLGN, RDG, JG, PK & MJV contributed to the conceptualization and analysis of data.

RLGN, AC, LSC & MJV contributed to the interpretation of results.

RLGN wrote the first draft of the manuscript.

All authors contributed to the writing of the manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

The supplementary material includes additional tables and figures cited throughout the paper and detailed methodology regarding delineation of catchment area, statistical analysis and computation of volume and precipitation data for each lake. https://doi.org/10.1016/j.scitotenv.2020.137044.

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Chapter 2

PHYTOPLANKTON COMMUNITY COMPOSITION AND STRUCTURE DIFFERS AMONG TROPICAL LAKES AND RESERVOIRS

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Abstract

Water bodies with different origins, natural or artificial, can greatly differ in their morphological features, landscape characteristics and surrounding land use. These differences may influence their biological communities. The aim of this study is to characterize lakes and reservoirs regarding the landscape properties of their surrounding areas (i.e. catchment size and catchment land use absolute and relative extent), their morphometry (i.e. ecosystem size, lake perimeter to lake volume ratio - LP:LV, and catchment area to lake volume ratio – CA:LV) and their physico/chemical characteristics, and verify whether those factors can be associated with average patterns of phytoplankton community structure at both local and regional scales across 98 lakes and reservoirs in Northeast Brazil. Reservoirs presented, on average, higher extension of anthropogenic land use as well as higher CA:LV than lakes, indicating that these systems are more prone to receive allochthonous material. Although reservoirs were more productive than lakes on average, this higher trophy was not associated with higher phytoplankton biomass. Relative biovolume of cyanobacteria and total biovolume of toxic cyanobacteria was greater in reservoirs when compared to natural lakes but it does not seem to be associated with a strong selection of more tolerant species, as there was no difference on average local species dominance. Our results show that lakes and reservoirs did not differ regarding local diversity patterns, but they presented different community composition. In addition, we found that reservoirs are important systems promoting phytoplankton diversity as they had higher gamma diversity, probably due to the higher number of exclusive species. When both lakes and reservoirs systems were combined, they held a greater regional species richness than the two types of ecosystems alone, suggesting that complementarity in species composition among these two types of ecosystems is a fundamental factor to the large-scale patterns in phytoplankton diversity.

Key words: Shallow lakes, drylands, eutrophication, lake morphometry, land use

1. Introduction

It is estimated that natural lakes (hereafter lakes) and human made reservoirs (hereafter reservoirs) larger than 0.1 Km^2 represent only 1.8% and 0.2% of global land surface, respectively (Messager et al., 2016). Despite this small proportion, lakes and reservoirs hold about 90% of world's surface fresh water (Herschy, 2012), constituting a vital resource (Katsiapi et al., 2012). Their good water quality is fundamental to the maintenance of a variety of ecosystem services such as the drinking water provision, biodiversity conservation, climate regulation, fishery and recreation (Williamson *et al.*, 2009; Carpenter, Stanley & Vander Zanden, 2011; IPBES, 2018).

The role of freshwater systems in the global hydrological and biogeochemical cycles is strongly related to geomorphological features of these water bodies such as surface area, volume, depth and perimeter (Messager et al., 2016). This happens as lake size and shape are associated not only with transport processes, e.g. sedimentation, internal loading and outflow (Hakanson, 2005a), but also with the connectivity of the lake with its surrounding habitat, regulating the amount of allochthonous material entering the systems (Baker, 2003; Hakanson, 2005). Interactions of these parameters with characteristics of the surrounding landscape, such as catchment land use and size, can in turn affect water abiotic and biotic parameters that are often descriptors of water quality including the concentrations of nutrients and suspended solids and nuisance algal blooms (Cardille et al., 2004; Foley et al., 2005; Vanni et al., 2011). Consequently, these changes can affect freshwater ecosystem's health, including their productivity and biodiversity (e.g. species richness, abundance and composition) at both local and regional scales (Cabral et al., 2019; Doubek et al., 2015; Mantzouki et al., 2015; Schindler, 2006).

Those differences in spatial features of aquatic ecosystems (and thus, on ecosystem structure and function) can arise when considering water bodies with different origins, such as natural lakes and artificial reservoirs (Doubek and Carey, 2017; Thornton et al., 1981). While lakes are natural features of the landscape originated from geologic time and forces (Thornton, 1984), reservoirs are artificial man-made water bodies, often presenting intermediate characteristics between lakes and rivers. Consequently, reservoirs are newer than lakes, since most of them were constructed in the past 60 years (Lehner et al., 2011) with the objective to store water for multiple purposes, specially where water availability is scarce (Soballe and Kimmel, 1987; Thornton, 1984). Compared to lakes, reservoirs usually present greater catchment size because dams are strategically built along higher order rivers to allow damming of water from a large catchment area. Reservoirs are also built in places with more rugged topography, and therefore, they usually also present higher depths (thus, greater volume), perimeter and consequently higher catchment area to lake volume (CA:LV) and perimeter to lake volume (LP:LV) ratios, which may determine a higher potential influence from terrestrial sediments and nutrients entering reservoirs (Doubek and Carey, 2017; Knoll et al., 2015; Menezes et al., 2018; Thornton, 1984). Additionally, because reservoirs are constructed for human use, they are often embedded in a context of anthropogenic land use (e.g. farming or urbanization), which make them more susceptible to non-point sources of pollution and other sources of degradation than natural lakes Kimmel, 1990; Knoll et al., 2003).

Examinations of the structure of planktonic communities has been a central goal in ecological studies (Soininen et al., 2011; Stomp et al., 2011; Watson et al., 1997). Because microorganisms such as phytoplanktonic groups presents small size and large population densities (Finlay, 2002) they are usually considered to be cosmopolitan. Thus, their community are usually structured by local ecological determinism, but large-scale forces such as dispersal can play a role when studying community structure on regional scales (Soininen et al., 2011). Indeed, phytoplankton communities across inland aquatic ecosystems have shown that local environmental factors such as light intensity, mixing regime, water residence time and lake morphometry are key factors related to community structure and composition (Beaulieu et al., 2013; Costa et al., 2018; Tamar et al., 2010). Additionally, it has long been recognized that conversion of natural landscapes to anthropogenic land uses as urban areas, pasture and agriculture have the potential to indirectly affect planktonic community structure and composition (Doubek et al., 2015; Mantzouki et al., 2015; Schindler, 2006) as those changes often affect the absolute and relative (i.e. stoichiometry) inputs of nitrogen (N) and phosphorus (P) to waterbodies, the main elements controlling primary productivity in freshwater systems.

This artificial over-enrichment of freshwaters promotes eutrophication which can leads to an increase in phytoplankton biomass (Reynolds, 1987) and also impoverish phytoplankton community composition and diversity by favoring the occurrence and dominance of phytoplanktonic groups such as cyanobacteria (Elliot et al. 2006, Paerl and Paul, 2012, Brasil et al. 2016, Costa et al. 2016). Cyanobacterias are an extremely heterogeneous group with many genera presenting adaptive advantages to survive under anthropogenic modified systems, enabling them to develop their communities in a span of different nutrient level environments (Paerl and Otten, 2013), and often they end up to dominate other planktonic and benthic communities where they occur. The dominance of this group in the ecosystems they occur is often related to a series of negative ecological and economic impacts (Bonilla et al., 2016; Doubek et al., 2015; Hamilton et al., 2013). In addition it is important to consider that a great proportion of cyanobacteria are known for producing a variety of toxins, including neurotoxic compounds which can be harmful for wildlife and humans (Azevedo et al., 2002; Doubek et al., 2015).

Recognizing the importance of distinct environmental contexts related to lakes and reservoirs can be fundamental to understand their health and the structure and conservation of biological communities living in these systems (Hakanson, 2005). This is especially true in the recent context of the Anthropocene, where human actions and global climatic changes combined are leading to a reduction in the number of natural lakes and an increase in the absolute and relative number of reservoirs on the landscape (Pekel et al., 2016). These changes are even more prominent in the dryland regions of the globe where water scarcity, due to more frequent and prolonged droughts, imposes the need for water storage solutions (Marengo et al., 2016; Pekel et al., 2016).

In this sense, the goal of this study is to characterize lakes and reservoirs regarding the landscape properties of their surrounding areas (i.e. catchment size and catchment land use absolute and relative extent), their morphometry (i.e. ecosystem size, and P:LV and CA:LV ratios) and their physico/chemical characteristics, and verify whether those factors can be associated with average patterns of phytoplankton community structure at both local and regional scales across 98 lakes and reservoirs in Northeast Brazil. Because reservoirs are more embedded in anthropogenic landscapes and usually present morphometric and landscape characteristics that are associated with higher allochthonous nutrient inputs and concentration (i.e. higher eutrophic conditions), (*i*) we expect they present, on average, phytoplankton communities with higher total biomass and higher absolute and relative cyanobacteria biomass than lakes (Brasil et al., 2016; Jeppesen et al., 2007; Menezes et al., 2018); In addition, since more eutrophic and hypereutrophic conditions can function as ecological filters selecting tolerant species. (*ii*) phytoplanktonic communities of reservoirs should present, on average, higher local species dominance (i.e. lower evenness) and lower local species diversity (Paerl and Otten, 2013; Paerl and Paul, 2012). (*iii*) Reservoirs are also expected to present lower regional (gamma) diversity than lakes because eutrophication is also usually associated with biotic homogenization of metacommunities (Monchamp et al., 2018; Wengrat et al., 2018). In counterpart, natural lakes, which are usually older and more oligotrophic systems than reservoirs, should present, on average, higher biological diversity as they had more time to be colonized and to develop higher levels of structural complexity that could embrace different functional traits leading to more diverse local and regional communities (Cabral et al., 2019; McKindsey and Bourget, 2001; Pianka, 1988). Finally, we expect that the aforementioned distinctions of local and catchment level environmental characteristics of lakes and reservoirs will select, on average, more regional similar species composition within each ecosystem type, resulting in a regional species complementarity between lakes and reservoirs. Thus, (*iv*) we also expect phytoplanktonic gamma diversity of lakes and reservoirs alone should be smaller than when both ecosystem types are combined.

2. Methods

Study area

The study was conducted across 98 perennial lentic freshwater systems, 30 lakes and 68 man-made reservoirs, located in the state of Rio Grande do Norte, northeastern Brazil (Fig. 1). Location of these systems expands from the coastal to the semi-arid region with 68% of the studied ecosystems located in a semi-arid region (annual precipitation ≈ 400-800 mm) and the remaining ecosystems distributed along the coastal region within a sub-humid and humid climate (annual precipitation ≈ 800-1200 mm) (BSh climate, Köppen classification). This large spatial distribution of studied aquatic systems spans not only a climatic gradient, but also a gradient of catchment land use and trophic state, ranging mostly from pristine forested areas to agricultural land cover and from oligotrophic to hyper-eutrophic conditions (Cabral et al., 2019; Junger et al., 2019).The majority of the systems are small and shallow (90% with depth < 4m; 89% < 1km^2 of surface area, Table 1).

Most of the systems located in the semi-arid region are artificial reservoirs (85%), while at the coastal humid climate, 35% of the water bodies are natural and 65% are artificial lakes. The man-made lakes sampled in this study were formed between 1915 and 1950 by stream damming conducted by the National Department of Works for Drought Control (DNOCS, 2015) with the goal to store water that serves to multiple purposes (e.g. drinking, agriculture, fishing). During most of their hydrological cycle, those systems present a negative water balance associated to low outflow, high water residence time and high temperatures (Barbosa et al., 2012; Menezes et al., 2018).

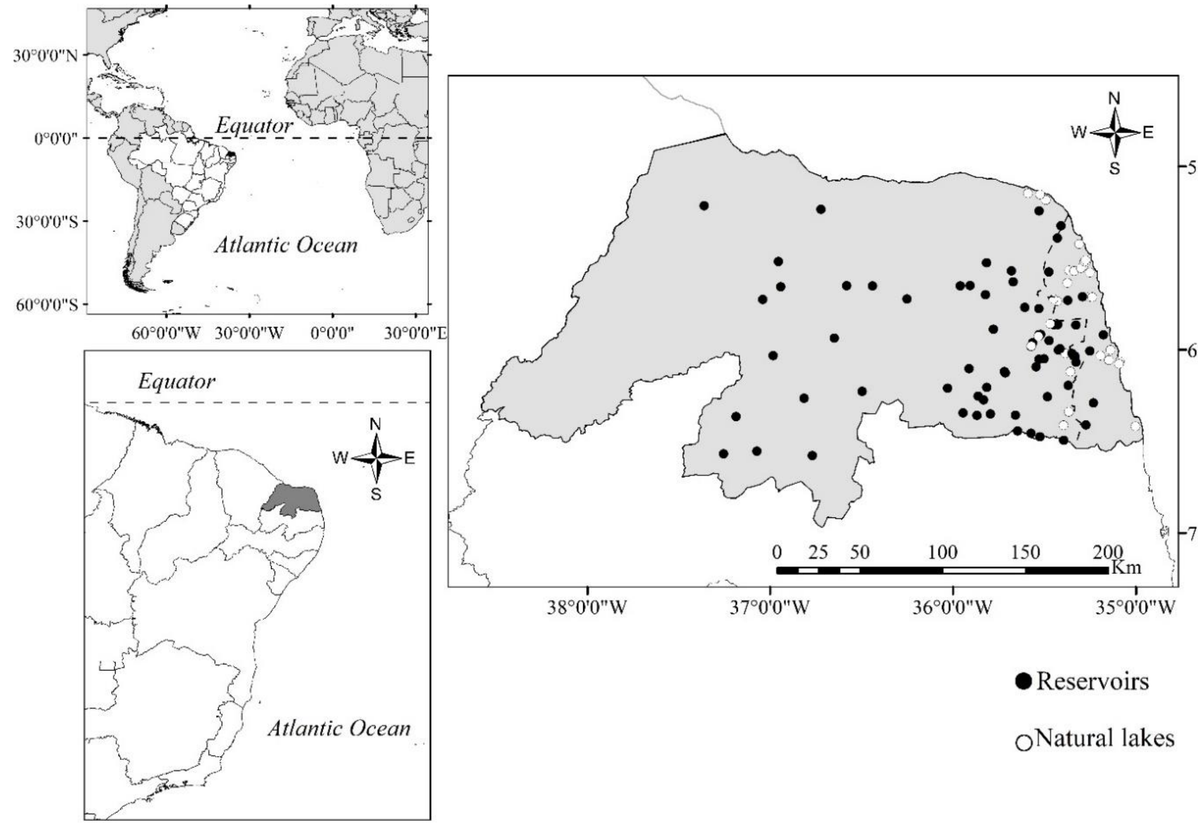

Fig. 1 – Map indicating the location of the 98 lakes (white dots) and reservoirs (black dots) distributed across the state of Rio Grande do Norte, Brazil. The dashed line depicts the semi-arid delimitation according to SUDENE (2017). To the right of the line is the coastal humid region and to the left is the semi-arid.

Additionally, the soil on its surroundings are mostly shallow and low-permeable, preventing groundwater accumulation. Reservoirs in the semi-arid region usually present a large catchment area-to-surface are ratio, which makes their water quality and biological communities more susceptible to the effects of catchment properties as for instance, catchment land use (Thornton & Rast, 1993, Junger et al. 2019). On the other hand, most natural lakes are coastal systems usually supplied by groundwater (Esteves et al., 2008) originated from the tertiary period with subsequent quaternary sediment deposition, situated in sand dunes and in deep soils with low fertility compared to the more fertile soils of the semi-arid region (Brito, 2010, Cabral et al. 2019).

Table 1 – Morphometric characteristics for sampled lakes and reservoirs

	Lake area (Km²)	Lake perimeter (m)	Lake depth (m)	Lake volume (m³)	Catchment area (Km²)
Lakes (n=30)					
Mean	0.39	2386.86	1.60	374293.66	1.63
±SD	1.30	3952.12	0.85	1408530.53	2.45
Max	7.25	22691.57	4.00	7798792.55	10.35
Min	0.00	219.86	0.20	1781.85	0.07
Reservoirs (n=68)					
Mean	0.94	6544.20	2.05	1052216.72	184.42
±SD	2.31	11585.90	1.20	2936994.14	437.49
Max	13.29	54448.19	4.50	17878648.09	2043.20
Min	0.00	219.18	0.20	1372.14	0.62

Field sampling of environmental variables and phytoplankton community

All 98 ecosystems were sampled during the dry season (September) of 2012. In order to obtain a physical/chemical characterization of lakes and reservoirs a set of abiotic variables were measured in the field. For each ecosystem light availability (Secchi disc), depth of euphotic zone (2.7 x Secchi disc depth; Esteves, 2011), temperature (portable digital probe – MO900/Instrutherm) and pH (bench855 top pH meter – MS Tecnopon®/mPA 210) were measured in the limnetic region of the aquatic systems. To determine the concentrations of total phosphorus

(TP), total nitrogen (TN), nitrogen to phosphorus ratio (N:P) and phytoplankton community, water samples were collected from the subsurface portion (approximately 0.3 m deep) of the water column of each lake with a Van Dorn sampler. Samplings were performed at six points in littoral and limnetic habitats (3 per habitat) and integrated into a single sample per water body. Those samples were then analyzed in the laboratory for TN and TP (Valderrama 1981) and characterization of phytoplankton community. Determination of TN (mgL^{-1}) was done by a carbon analyzer (TOC-V) coupled with a nitrogen analyzer (VPN module) and an autosampler (Shimadzu). Total phosphorus (mgL^{-1}) was determined by persulfate oxidation and measured by reactive soluble phosphorus method (Murphy & Riley 1962).

Phytoplankton samples were counted in random fields using an inverted microscope (Utermölh 1958; Uhelinger 1964), until 100 individuals (cells, filaments or colonies) of the most abundant species (Lund et al. 1958) were reached and the species accumulation curve was saturated. Identification and classification of phytoplankton species were conducted by following the major taxonomic schemes from the Integrated Taxonomic Information System (itis.gov), Tree of Life database (tolweb.org) and Adl et al. (2012), except for Cyanobacteria which were identified by using specific taxonomic guides (Komárek et al. 2014). To obtain phytoplankton biovolume (mm^3L^{-1}), the cell volume was calculated by approximations to similar solid geometric shapes (Hillebrand et al., 1999). Three major groups were used in this study to compare phytoplankton community in lakes and reservoirs: total phytoplankton, cyanobacteria and potentially toxic cyanobacteria. In other to calculate biodiversity metrics (rarefaction curve, Simpson's index and evenness), phytoplankton community data were expressed through species abundance (individuals/mL), while to compare total and relative biomass of phytoplanktonic groups among lakes and reservoirs phytoplankton biovolume was used.

Landscape and land use properties

To better characterize lakes and reservoirs regarding morphometric characteristics of the aquatic systems and their catchments, as well as the patterns of land use on its surrounds, lake surface area and perimeter, were calculated through satellite image processing (delineation of polygon shapefiles) using ArcGIS 10.5 (ESRI, 2017). Lake depth was measured at the central part of each lake using a calibrated rope, and lake volume was calculated through the hyperbolic function 0.43 × lake area × depth (Post et al., 2000).

To verify whether there are differences on the patterns of land use (extension of anthropogenic land use and distance of use) between lakes and reservoirs, which in turn may affect phytoplankton communities, total catchment areas and “buffer zones” (i.e. near-freshwater land zone around the water body comprising a distance of 100-meter from its shore) were delineated for each lake and extension of anthropogenic land use on the catchment and on the buffer scale were obtained (total area in Km^2). The delineation for each one of the 98 lake’s catchments were based on the water bodies polygon shapefiles and it was performed using ArcHydro 2.0 Toolbox (ArcHydro, 2011) on ArcGIS 10.5 (ESRI, 2017). Detailed methodology for catchment delineation can be found in Cabral et al. (2019). Morphometric landscape properties such as catchment and buffer area were calculated in ArcMap 10.5 (ESRI, 2017). Catchment area-to-lake volume ratio (CA:LV), buffer area-to-lake volume ratio (BA:LV) and lake perimeter-to-lake volume ratio (LP:LV) were also calculated because they are expected to influence the connectivity on the land-water interface.

Land use for each lake buffer and catchment was obtained by using 2012 data available through Project MapBiomas - Collection 3 of Brazilian Land Cover & Use Map Series (Projeto MapBiomas, 2018). Total area of each land use type was calculated on ArcGIS 10.5 using the tabulate area function. Subsequently, categories of land use provided by MapBiomas were grouped within the main class "anthropogenic use". Anthropogenic use includes urban/developed zones and agriculture areas (cropland and pasture). They were grouped as these types of land use are expected to have similar effects on the increase of nutrient inputs on waterbodies (Foley et al., 2005) that may reverberate in effects on phytoplankton communities.

Statistical analysis

For statistical purposes of normality improvement and/or to meet homogeneity of variances all variables were log10(x+1) transformed before analysis. Homogeneity of variances was tested for each environmental variable using Levene's test. Average differences in physical/chemical parameters as well as differences in landscape and land use properties between lakes and reservoirs were tested using Student's t test to compare TN, TP, N:P, anthropogenic land use on the catchment and on the buffer scale, CA:Vol, BA:Vol and LP:Vol (homogeneous variances among samples) and Mann-Whitney test to compare water pH (non-homogenous variances among samples).

To investigate if reservoirs supported on average, a higher total and relative biomass of phytoplanktonic groups than lakes, we used unpaired Students' test to compare total biovolume of phytoplankton, total biovolume of cyanobacteria and relative biovolume of cyanobacteria, and Mann-Whitney test to test differences among lakes and reservoirs regarding the relative biovolume of cyanobacteria and the total biovolume of toxic cyanobacteria. Student's t test and Mann-Whitney test were performed in R using the *stats* package (R Core Team, 2019). The corresponding graphs were produced using GraphPad Prism 7.04.

Local phytoplankton biodiversity metrics used to compare lakes and reservoirs were Simpson's diversity index (compared with Student's t test), phytoplankton species evenness and richness (compared with Mann-Whitney test). To test weather regional species richness (gamma diversity) differed among lakes and reservoirs (and from all 98 lakes together), individual-based rarefaction curves were used. For details regarding this method, see Cabral et al. (2019). Briefly, the bootstrap (with 1000 iterations) method was used to construct the rarefaction curves by randomly selecting the individuals according to a growing sampling effort. The routine for individual based rarefaction curves was written by the authors and can be found on the supplementary material. To investigate whether lakes and reservoirs differed in their phytoplankton species composition, a permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) based on both, the Jaccard index (presence/absence) and Bray-Curtis dissimilarity matrix (abundance) were performed. Simpson's index of diversity and evenness, as well as PERMANOVAs were calculated using the vegan package (Oksanen et al. 2015) in R version 3.6.1 (R Core Team, 2019). In order obtain a graphic of phytoplankton community composition, Nonmetric multidimensional scaling (NMDS) with a Jaccard similarity matrix was performed in R using the standard function metaMDS in the vegan package (Oksanen *et al*. 2015).

3. Results

Across the 98 lakes studied, it was observed some significant differences in land use and landscape properties as well as on chemical and biological characteristics between lakes and reservoirs. Concerning the landscape and land use properties, the extent of anthropogenic land use on the catchment was on average higher for reservoirs than lakes (Figure 2a), but lakes presented a slightly higher proportion of human land use on the catchment scale (Figure 2c). Reservoirs also presented higher catchment area to volume ratios (Fig. 2e). No significant differences among the two types of ecosystems were observed for the extent or proportion of land use on the buffer scale, buffer area-to-volume ratio or lake perimeter-to-volume ratio (Fig.2, panels b, d, f and g, respectively).

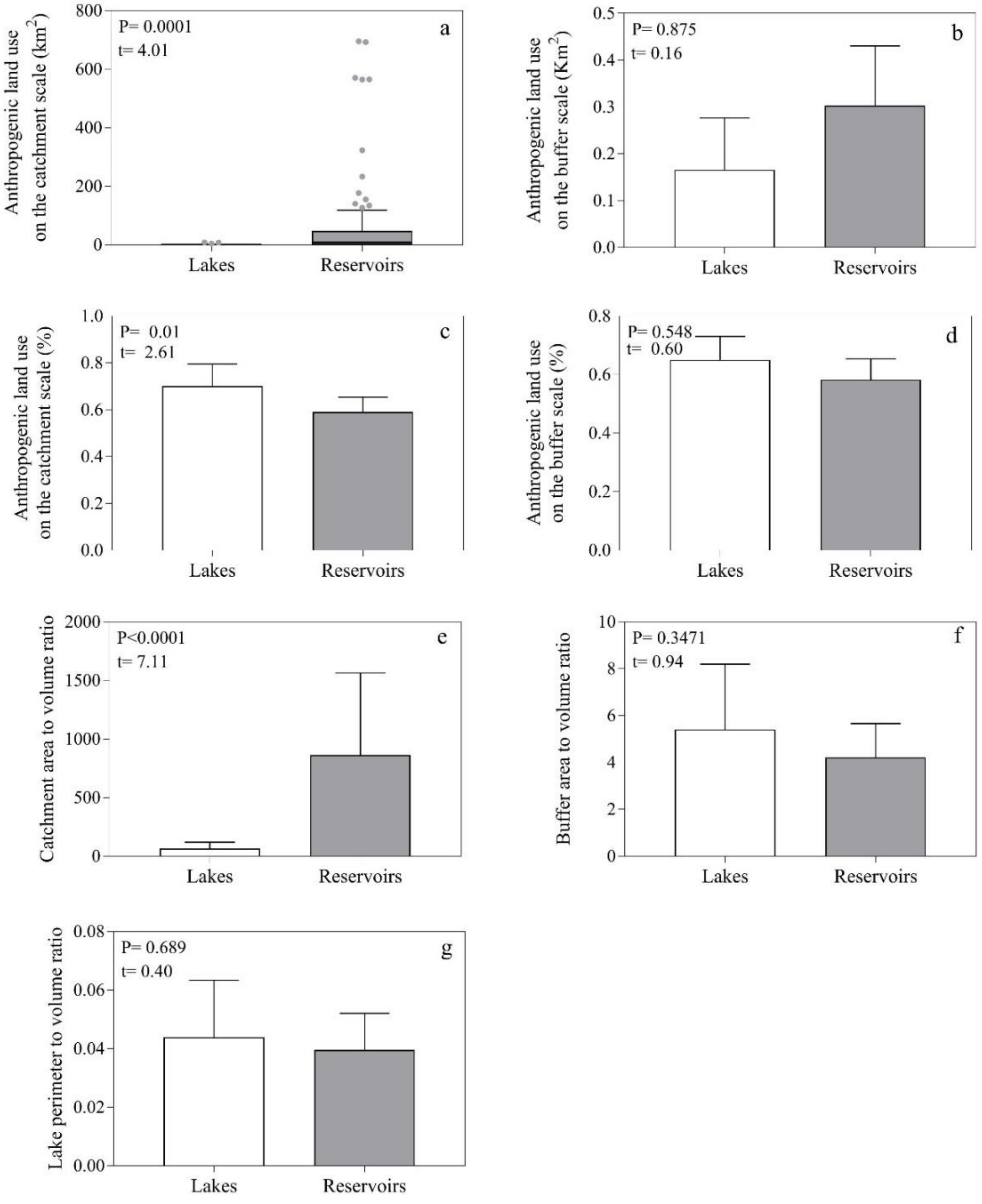

Fig. 2 Comparisons of landscape and land use properties among lakes (n=30) and reservoirs (n=68). **a.** Extension of anthropogenic land use on the catchment scale; **b**. Extension of anthropogenic land use on the buffer scale; **c.** Catchment area to volume ratio; **d.** Buffer area to volume ratio; **e.** lake perimeter to volume ratio. Differences on the average values of the mentioned

variables were tested with Student's t test. Columns and vertical bars depict the mean and ± 95% confidence intervals.

Lakes and reservoirs presented differences among the parameters used to describe its physico/chemical characteristics. Reservoirs showed on average higher concentrations of TN, TP and higher values of pH (Fig. 3, panels a, b and e respectively), while the depth of euphotic zone was higher for lakes (Fig. 3d). There was no significant difference among the two types of ecosystems regarding the average values of N:P ratios or temperature (Fig. 3, panels c and f).

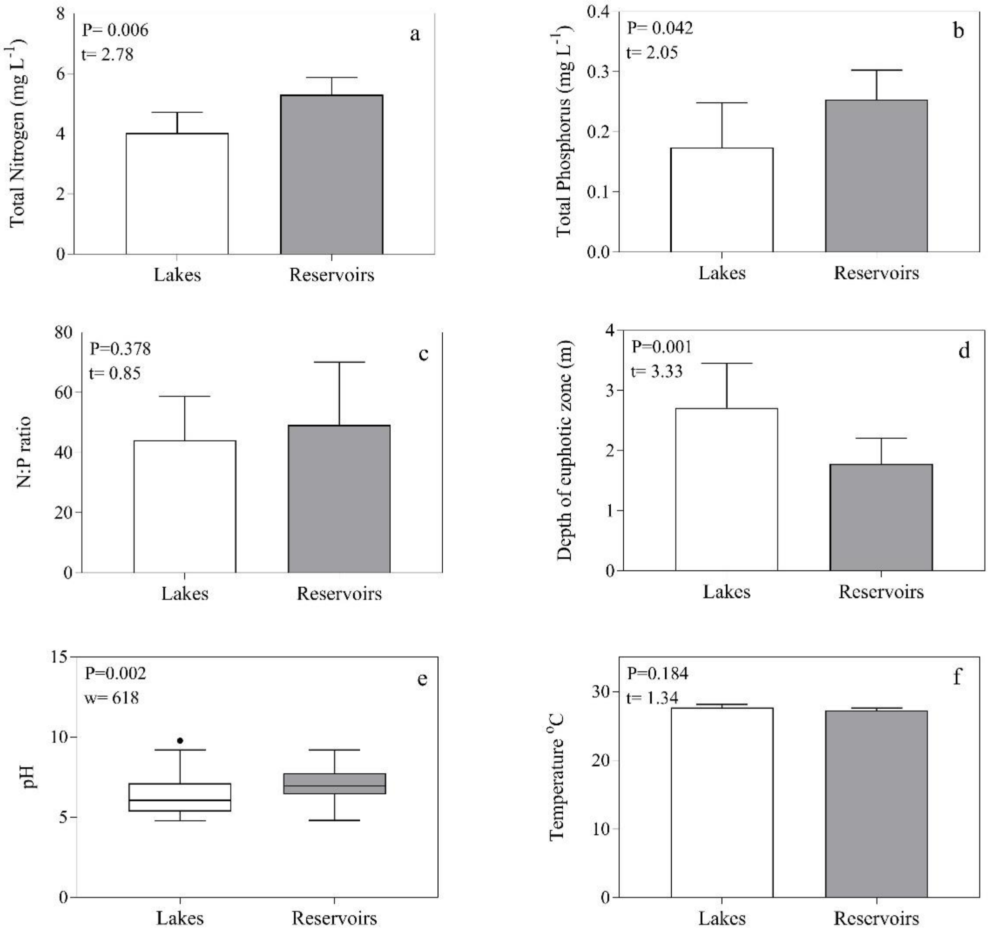

Fig. 3 Comparisons of physio/chemical parameters among lakes (n=30) and reservoirs (n=68). **a.** TN; **b**. TP; **c.** N:P ratio **d.** Depth of euphotic zone; **e.** pH; **f.** Temperature. Differences on the

average values of TN, TP, N:P, depth of euphotic zone and temperature were tested with Student's t test. Columns and vertical bars depict the mean and ± 95% confidence intervals. pH was tested through a nonparametric Mann–Whitney test. Boxes and horizontal bars represent the interquartile range, median and the data range, respectively.

It was recorded a total of 307 phytoplankton species across the 98 ecosystems. In reservoirs, 245 species were registered, and from that total, 131 species (42%) were exclusively found in these systems. Lakes presented a total of 135 phytoplankton species, with 62 species occurring only in lakes. Lakes and reservoirs shared 114 species. Euglenophyceae was the group with higher biovolume in lakes (36% of total phytoplankton biovolume) followed by Cyanophyceae (34%) and Zygnemaphyceae (13%), while in reservoirs the taxonomic groups representing the higher proportions of the phytoplankton biovolume were Cyanophyceae (53%), Chlorophyceae and Euglenophyceae (6%).

When considering alpha diversity, there was no differences between lakes and reservoirs regarding Simpson's diversity, species evenness, and the average local species richness (Fig. 4, panels a to c, respectively). Additionally, no differences between systems were found for total phytoplankton biovolume (Fig. 4d).

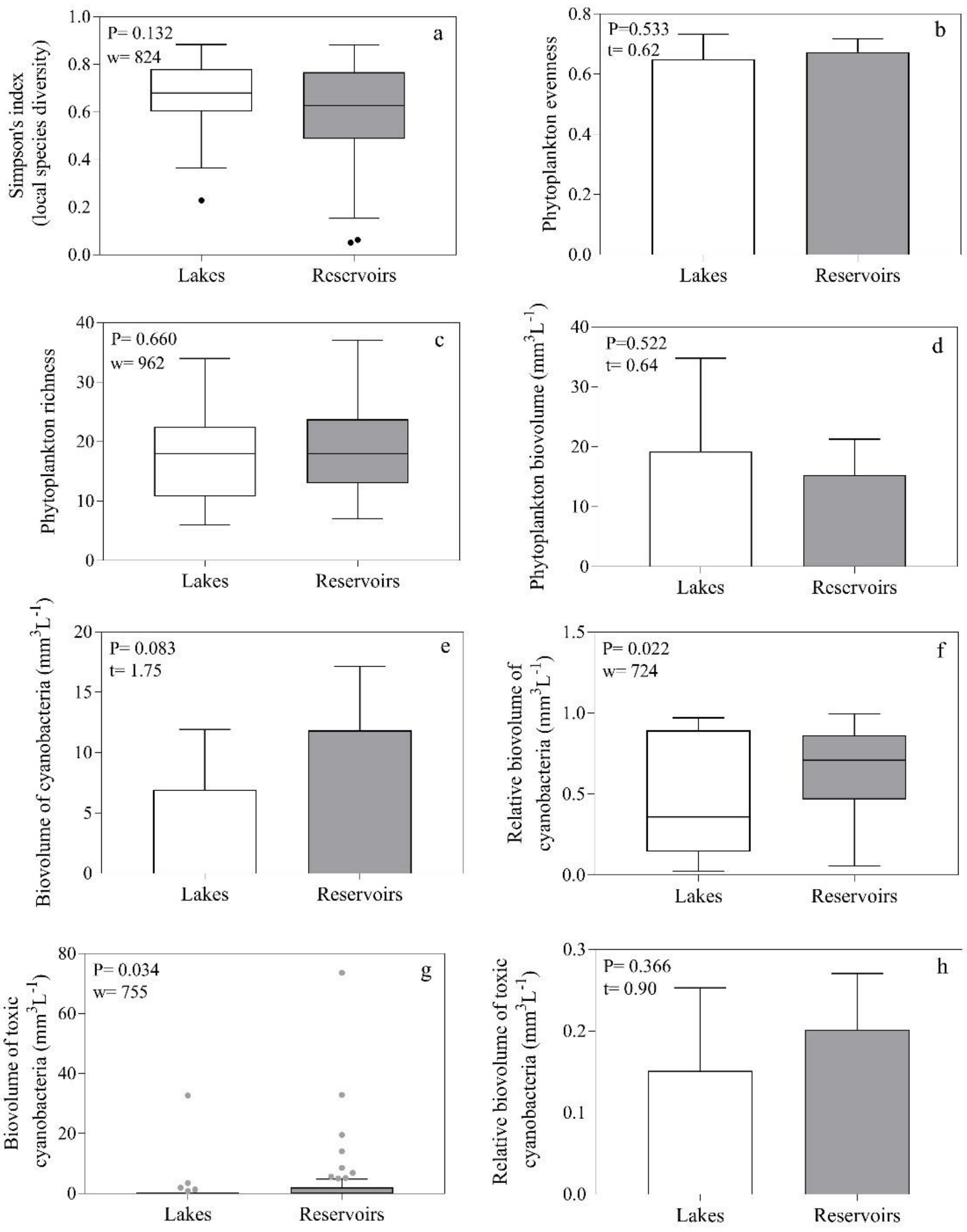

Fig. 4 Comparisons among lakes (n=30) and reservoirs (n=68) regarding the local average phytoplankton **a.** species diversity (Simpson's index); **b**.species evenness; **c.** Species richness; as well as **d.** phytoplankton biovolume; **e.** cyanobacteria biovolume; **f.** relative cyanobacteria biovolume; **g.** toxic cyanobacteria biovolume and **h.** relative toxic cyanobacteria biovolume. Differences on the average values of a, c, f and g were tested with Mann – whitney test. Boxes and

horizontal bars represent the interquartile range, median and the data range, respectively. Averages of all other variables were teste through student's t test. Columns and vertical bars depict the mean and ± 95% confidence intervals.

Although there was not significative difference among the average biovolume of cyanobacteria between the two types of freshwater systems (Fig. 4e, p=0.08), reservoirs presented higher relative biovolume of cyanobacteria (Fig. 4f, p=0.02). When the average biovolume of toxic cyanobacteria was compared among systems, it was observed a higher biovolume of this group in reservoirs (Fig. 4g, p=0.03), however for the relative biovolume of toxic cyanobacteria there was no difference between lakes and reservoirs (Fig. 4f, p=0.36).

At low sampling efforts the regional species richness accumulated in a similar proportion for lakes and reservoirs, however, with increased sampling effort, reaching the maximum sampling effort for lakes (~ 300,000 ind.ml^{-1}), the Gamma diversity was higher for reservoirs than for lakes, meaning that proportionally more species of phytoplankton were found in those artificial systems (Fig. 5).

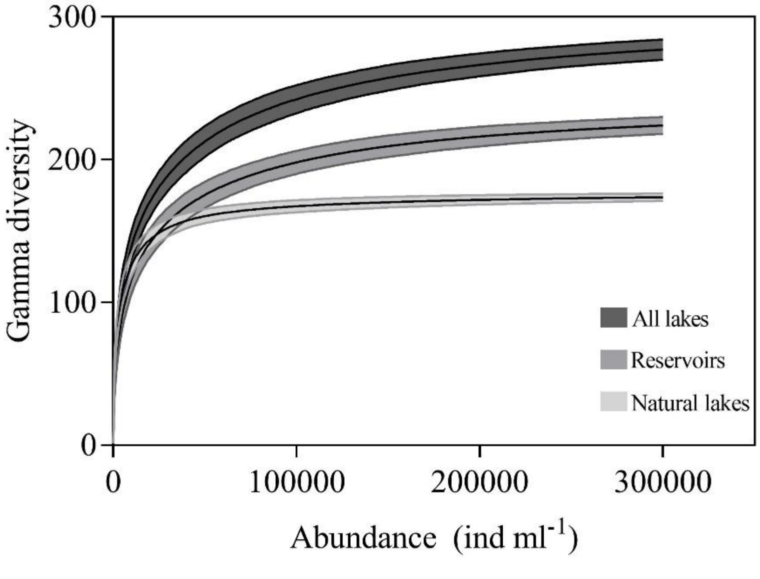

Fig 5 –Phytoplankton gamma diversity (regional species richness) for lakes (n=30), reservoirs (n=68) and all aquatic systems combined (n=98). Graphic shows individual-based rarefaction curves for the average (solid lines) accumulated phytoplankton species richness and their ± 95% confidence intervals (shaded areas). The scale of abundance is shown until that difference in species richness for lakes and reservoirs is stabilized.

Lakes and reservoirs showed different community composition (PERMANOVA; $F_{Jaccard} = 2.08$; p = 0.002; $F_{Bray\text{-}curtis}=2.41$, p =0.001). Although many species are present in both systems, there were some species that were exclusively found on reservoirs and others on natural lakes (NMDS, fig. 6).

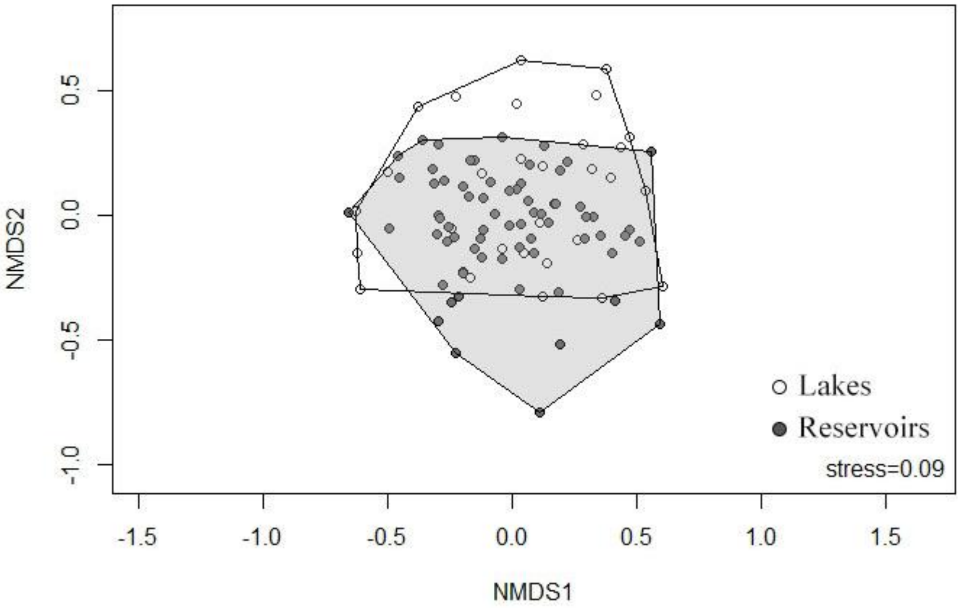

Fig. 6 - Nonmetric multidimensional scaling (NMDS) plots based on a Jaccard similarity matrix contrasting phytoplankton communities from lakes (n = 30) and reservoirs (n = 68).

4. Discussion

We found substantial differences in land use and landscape properties, water body morphometry, as well as physico/chemical and biological characteristics between lakes and reservoirs in the studied region. Reservoirs presented, on average, higher extension of anthropogenic land use as well as higher CA:LV than lakes, indicating that these systems are suitable to proportionally higher inputs of allochthonous material entering the system (Jones et al., 2008; Knoll et al., 2015; Menezes et al., 2018). Indeed, parameters related to lake productivity, such as TP, TN and secchi depth were markedly different between the two types of systems, with reservoirs tending to present, on average, higher concentrations of nutrients and lower depth of euphotic zone (indicators of higher trophy). Similar results were found by Jones and Bachmann (1978) who showed that lake origin is a factor associated with lake trophy.

Regarding our first hypothesis that reservoirs should present higher eutrophic conditions and consequently present, on average, phytoplankton communities with higher total biomass, we found that although reservoirs did present higher concentration of eutrophic indicators compared to lakes, this differential productivity was not associated with phytoplankton biomass (total and relative). As noted by Carvalho (1994), phytoplankton biomass is controlled not only by bottom-up mechanism but also by top-down processes such as predation. Additionally, assuming that both, lakes and reservoirs are submitted to similar predation pressures, the Fretwell-Oksanen hypothesis predicts that for ecosystems with even numbers of trophic levels (e.g. phytoplankton and zooplankton), herbivores would regulate primary producers rather than bottom-up mechanisms (Oksanen et al., 1981; Sinclair and Krebs, 2001). In fact, Cabral et al. (2019) studying this same set of ecosystems found that zooplankton abundance and biomass was on average, higher in reservoirs than in natural lakes, thus this high nutrient enrichment in reservoirs may be counterbalanced by a more intense herbivory pression in these systems.

We also predicted that more eutrophic conditions in reservoirs would lead to increased total and relative biomass of cyanobacterias in reservoirs than in lakes, and that this high trophy would function as an ecological filter selecting tolerant species, leading to higher local species dominance. As expected, the total biovolume of cyanobacteria was marginally greater in reservoirs and we also found a greater relative biovolume of cyanobacteria and total biovolume of toxic cyanobacteria when compared to natural lakes. However higher biovolume of cyanobacteria did not seem to be associated with a strong selection of more tolerant species, as there was no difference on average local species dominance. It is relevant to point out that a great proportion of the studied systems presented cyanobacteria concentrations higher than the limits established by the Brazilian national environmental council (CONAMA). According to the Resolution Nº 357/2005, water for human consumption should not exceed concentrations above $2m^3$ind-1, while water for multiple uses including fishing and animal consumption should not exceed $10m^3$ind-1. We found that 38% of the reservoirs and 10% of the natural lakes were above the human consumption limit, and 16% of the reservoirs and 6% of the lakes presented alarming cyanobacterias concentrations above 10 m^3ind-1.

Reservoirs located in the semi-arid region are especially susceptible to the occurrence of cyanobacterial blooms, and this situation can be aggravated in the context of future climate scenarios (Beaver et al., 2014; Paerl and Paul, 2012). In the last decades, the connection between climate change and the proliferation of algal blooms has also been demonstrated in several studies (Paerl and Otten, 2013). Because cyanobacteria are prokaryotic organisms, they tend to present higher growth rates under increased temperatures, while other eukaryotic groups of phytoplankton show stable or reduced growth rates when temperatures are above 20°C (Paerl & Huisman, 2008, Barros et al., 2019). Some cyanobacteria groups can also have buoyance mechanisms and adaptations to support high intensity of sunlight and UV exposure, which gives then competitive advantage under scenarios of increased temperatures (Barros et al., 2019).

The artificial enrichment of freshwaters combined with increased temperatures are thus expected to enhance cyanobacteria proliferation and dominance in freshwaters. Therefore, given that many of the water bodies sampled, specially the reservoirs located on the semi-arid region, are sources of water for multiples purposes, including human and animal consumption, it is fundamental to better understand the processes promoting cyanobacterial growth and dominance in the contemporary context of high habitat transformations (land use) and climate changes.

We further expected that in a scenario of higher trophy and higher species dominance in reservoirs, natural lakes should present higher local (Simpson's index and local species richness) and regional diversity. However, both systems showed similar levels of phytoplankton alpha diversity, but reservoirs presented higher gamma diversity. Like the conclusions of Cabral et al. (2019) studying zooplankton communities in the same set of ecosystems than the present study, we can also attribute the higher gamma diversity in reservoirs to the elevated number of exclusive species found in these systems (42%).

In addition, natural lakes sampled in this study are mostly located in the humid region, where levels of precipitation are higher than in the semi-arid. While reservoirs were mainly located in the semi-arid region, where droughts may impose hydrological isolation of aquatic systems. Brasil et al. (2019) suggested two main mechanisms by which planktonic communities may be structured in this same semi-arid region. The first mechanism proposes that higher levels of precipitation are associated with nutrients and biological communities' dilution, leading to higher homogenization of limnological parameters and consequently diminishing the variability in phytoplankton communities (Brasil et al., 2019). In opposition, droughts in the semi-arid region can lead to isolation of the aquatic systems (They et al., 2017), promoting higher spatial heterogeneity and limiting dispersal processes. As a consequence, phytoplankton communities are more diverse as they are locally forced to follow different trajectories (Brasil et al., 2019; Rojo et al., 2012). Although Brasil et al. (2019) did not find a significant effect of hydrological isolation on the structure of plankton metacommunities they also suggest that other dispersion processes, such as bird dispersion and human activities, may play a role in structuring semi-arid planktonic communities.

In accordance to the findings of Cabral et al. (2019), we found that despite the high trophy levels of reservoirs, they are important systems promoting phytoplankton diversity. As predicted, when both lakes and reservoirs systems were combined, they held a greater regional species richness than the two types of ecosystems alone. This result suggests that the regional phytoplankton diversity in the studied area is enhanced by the different species pool found in lakes and reservoirs and that complementarity in species composition among these two types of ecosystems is a fundamental factor to the large-scale patterns in phytoplankton diversity. Therefore, we support Cabral et al. (2019) recommendation to freshwater managers and policy makers, reinforcing that they must include scenarios with a combination of lakes and reservoirs in the landscape in order to preserve phytoplankton biodiversity in a regional scale.

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Chapter 3

Fish, Including Their Carcasses, Are Net Nutrient Sources to the Water Column of a Eutrophic Lake

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Fish, Including Their Carcasses, Are Net Nutrient Sources to the Water Column of a Eutrophic Lake

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Animals can act as sources or sinks of nutrients in ecosystems, and their role in this context may depend on the fate of nutrients in decomposing carcasses, which may contain recalcitrant structures such as bones. Our goal was to assess whether a fish population with high biomass is a source or sink of nutrients to the pelagic zone of a eutrophic lake over time scales ranging from days to 20 years. We developed a population-level model based on a 20-year (1996–2015) dataset for gizzard shad (*Dorosoma cepedianum*) in Acton Lake, a eutrophic reservoir in southwest Ohio, U.S.A. In addition, we used data from experiments that quantified nutrient mineralization rates from carcasses as functions of fish size and temperature. Nitrogen (N) and phosphorus (P) remineralization rates from carcasses increased with temperature and decreased with fish size. Over the 20 years, almost all (~99%) of the nitrogen (N) and phosphorus (P) produced as gizzard shad carcasses was remineralized back to the water column. At the ecosystem scale, carcass nutrient dynamics followed a seasonal pattern, with a net accumulation of carcass nutrients in winter but a net depletion of the carcass nutrient pool in summer, due to mineralization. Dynamics of carcass production and remineralization were strongly influenced by young-of-year fish (YOY), for both N and P, because the number of fish born varied considerably across years, YOY have high mortality rates, and YOY carcasses decompose rapidly. On an annual basis, in a few years biomass production was higher than mineralization, suggesting that in these years fish biomass may act as a nutrient sink at the annual scale. However, nutrient excretion by the population greatly exceeded sequestration of nutrients in biomass (living and dead). Because most of the nutrients consumed (and excreted) by this population are derived from the benthos, at the lake-wide scale and considering all fluxes, the population is a significant net source of nutrients to the pelagic habitat. Our model demonstrates the relevance of considering spatial and temporal scale as well as long-term population dynamics when studying the role of animals as nutrient sources or sinks.

Keywords: nutrient cycling, decomposition, nitrogen, phosphorus, mineralization

INTRODUCTION

Animal populations can be nutrient sources or sinks (Kitchell et al., 1975; Beasley et al., 2012; Barton et al., 2013; Atkinson et al., 2017; Subalusky and Post, 2018). In aquatic ecosystems, an animal population can act as a source of nutrients when releasing nutrients in available forms to other members of the ecosystem, and as a sink when removing nutrients from circulation in the ecosystem (**Figure 1**). Studies on nutrient cycling by fish (and other aquatic animals) have focused mostly on their role as a nutrient source through excretion (Atkinson et al., 2017; Subalusky and Post, 2018). However, because fish can represent a large proportion of animal biomass in many ecosystems (Barton et al., 2019), because they are long-lived compared to other organisms, and because their bodies contain recalcitrant tissues like bones and scales, it has been suggested that fish populations act as nutrient sinks in pelagic freshwaters (Kitchell et al., 1975; Sereda et al., 2008). The main ways in which a fish population can be a nutrient sink are (1) if biomass increases, i.e., when growth and reproduction exceed mortality, (2) if emigration from the ecosystem exceeds immigration to that ecosystem, and (3) if nutrients stored in carcasses are not mineralized back to the water column, but rather remain stored in sediments in a recalcitrant form for a long time (Vanni et al., 2013).

If animal biomass is relatively stable, the fate of carcasses may be especially important in determining whether animals are nutrient sources or sinks. In general, animal carcasses are nutrient-rich resources that generally decompose much faster than plant detritus (Barton et al., 2013, Benbow et al., 2019). However, vertebrate carcasses contain bone, a phosphorus (P)-rich component that decomposes much more slowly than other tissues (e.g., Parmenter and Lamarra, 1991; Subalusky et al., 2017). Thus, carcasses could represent a relatively long-term P sink, and if P is the limiting nutrient this could constrain primary production. In addition, carcasses are produced and deposited at various spatial and temporal scales, which can modulate their role as sources or sinks. For example, in some populations carcasses are produced in highly episodic mass mortality events, whereas in other populations mortality is more temporally constant or varies seasonally (Fey et al., 2015; Subalusky et al., 2017). Carcass deposition can also be spatially variable, producing nutrient hotspots in the landscape that influence soil, or sediment biogeochemistry and primary production (Bump et al., 2009; Keenan et al., 2018). More specifically, in aquatic ecosystems, carcasses of pelagic animals may sink to the sediments, out of the euphotic zone and away from pelagic primary producers; thus they can be a sink for the pelagic ecosystem, but whether they are depends on the rate at which carcass nutrients are remineralized and transported to pelagic primary producers (Beasley et al., 2012; Vanni et al., 2013).

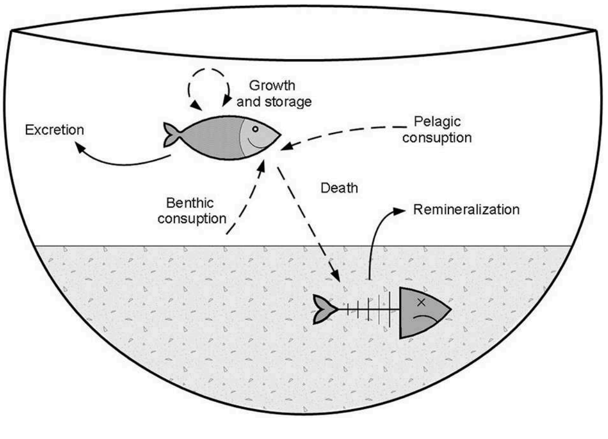

FIGURE 1 | Conceptual model showing the fluxes of nutrients derived from fish (sources to the water column, solid arrows) and stored in fish biomass (sinks from the water column, dashed arrows). Fish can act as nutrient sinks when they remove nutrients from circulation and store them in their bodies for growth, or when fish die and nutrients are stored in recalcitrant tissues. On the other hand, they act as sources of nutrients to the water column when they are releasing nutrients through excretion and remineralization of nutrients stored in carcasses. Piscivory is omitted here for simplicity.

In this paper, we assess whether a fish population with high biomass and growth rate is a source or sink of nitrogen and phosphorus to the pelagic zone of a eutrophic lake, at various time scales ranging from days to years. To accomplish this, we used a population-level model for gizzard shad (*Dorosoma cepedianum*) over a 20 year period in Acton Lake, a eutrophic reservoir in Southwest Ohio, U.S.A. Gizzard shad are abundant in lakes and reservoirs of the Midwest and southeast USA, and non-larval age classes feed mostly on organic detritus associated with sediments (Schaus et al., 1997; Higgins et al., 2006). Consumption of benthic-derived nutrients and subsequent excretion of these nutrients into the water column by gizzard shad represents an important nutrient source to phytoplankton (Shostell and Bukaveckas, 2004; Vanni et al., 2006; Schaus et al., 2010; Williamson et al., 2018). However, the role of nutrient storage in living fish and the fate of nutrients in carcasses is not well-known at the ecosystem scale. Our approach is comprehensive in that we explicitly quantified how this population can be a nutrient sink (storage in living biomass and carcasses) as well as a source (excretion, remineralization from carcasses) to pelagic primary producers, incorporating all life stages (including larvae) over a 20-year period.

METHODS

Population Model

We used the gizzard shad population model of Williamson et al. (2018), which estimated fish population size and age structure for multiple cohorts over a 20-year period (1996–2015). The model combines data from electrofishing, hydroacoustics, and larval fish sampling, to track the number and size of fish in each age class, and ultimately the mass of nutrients sequestered in living biomass and produced as carcasses, on a daily basis. Details of the population model are described in Williamson et al. (2018). Briefly, the number of larval fish was estimated using weekly tows with an ichthyoplankton or neuston net during the period of larval production (generally, May-June), for all 20 years. This allowed us to estimate the number of fish born each year, following methods of Bremigan and Stein (2001).

Non-larval fish were sampled each August (1999–2015) using hydroacoustics (Hale et al., 2008), which allowed us to annually estimate population size and age-structure. We do not have hydroacoustics estimates for 1996–1998; to obtain population estimates in August of each of these 3 years, we used a regression between electrofishing data (catch per unit effort, CPE) and hydroacoustics estimates developed for years in which we have both types of data (Williamson et al., 2018). Thus, for young-of-year (YOY) fish, we had estimates of cohort density (no. YOY fish per ha) during the hatching period (May–June) and in August, and for non-YOY fish we had estimates each August. The number of fish present in each cohort (ages 0, 1, 2, 3, and 4+ years) on each day in between population estimates was interpolated using daily instantaneous mortality rates, as described in Williamson et al. (2018). Fish size (wet mass) was obtained from larval fish tows, hydroacoustics and electrofishing, and interpolated on a daily basis (Williamson et al., 2018). Mortality, i.e., the number of fish in each cohort dying each day, was estimated by difference in cohort density on successive dates; this assumes no immigration or emigration in this population. We assumed that piscivory accounted for 15% of the mortality of gizzard shad smaller than 200 mm total length, when temperature was $> 10^\circ$C; for fish $>$200 mm, and for all fish when temperature was $<10^\circ$, we assumed no piscivory. These assumptions are based on piscivory estimates for largemouth bass and other piscivores in Acton Lake (Aman, 2007). Fish that died but were not consumed by piscivores were assumed to sink to the sediments as carcasses.

Nutrient Pools and Fluxes

Using data on the number and size of fish in each cohort, we estimated the mass of nutrients (N and P) in live fish biomass, and "lost" from the pelagic zone due to mortality on a daily basis. We also considered nutrients excreted by fish in the water column, using data from Williamson et al. (2018).

For each cohort, we modeled pools of carcass N and P as the balance of daily carcass production (mortality not due to piscivory) vs. mineralization. For each cohort, carcass production (no. carcasses produced ha^{-1} d^{-1}) was converted to nutrient mass produced as carcasses (g N and P ha^{-1} d^{-1}). To do so, fish wet mass was first converted to dry mass, and then to N and P mass using size-specific data derived from the Acton Lake gizzard shad population (Schaus et al., 1997; Pilati and Vanni, 2007; Torres and Vanni, 2007).

Remineralization of nutrients from gizzard shad carcasses was estimated using data from lab experiments that quantified nutrient mineralization rates from carcasses of different sizes, incubated at three temperatures (5, 15, and 25°C). Details on these experiments can be found in the **Supplemental Material**; briefly, we incubated YOY and adult carcasses at these three temperatures and measured their nutrient contents on several dates for up to 100 days (or shorter if carcasses fully decomposed). Based on these experiments, we calculated the decay rate (k) of carcass N and P by fitting the equation $M_t = M_0 e^{-kt}$, where M_t and M_0 are the masses of the element (N or P) remaining in carcasses at time t (days) and k is the instantaneous daily decay rate. Then we used two-way analysis of variance (ANOVA) to evaluate the individual and interactive effects of fish size and temperature on decay rates (k) for carcass N and P. When ANOVA detected significant effects of the experimental factors, we used Tukey's post-test for multiple comparisons to discriminate significant statistical differences between levels of experimental factors.

To estimate daily mineralization rates as a function of lake temperature, for each fish size class, we used Q_{10}, defined as the factor by which a decay rate increased when temperature increased by 10°C. This factor is commonly used in studies testing the temperature effects on biological rates (Lloyd and Taylor, 1994; Downs et al., 2008). For example, if a rate doubles when temperature is increased from 5 to 15°, the $Q_{10} = 2$. The values of Q_{10} for N and P decay rates for YOY and adult carcasses were estimated by using the k values computed previously; we calculated separate Q_{10} values for 5–15° and 15–25°. Q_{10} values for adult carcasses were used for all non YOY age classes. Cohort carcass mineralization rates were summed to obtain carcass mineralization rates at the lake-wide scale. We assumed that all nutrients mineralized from carcasses were returned to the water column in dissolved inorganic form and therefore were a nutrient source to phytoplankton; i.e., we assumed no benthic uptake of nutrients remineralized from carcasses. We feel that this is a valid assumption because Acton Lake is turbid and very little light reaches sediments (Secchi depth usually $\sim$0.5–0.7 m); therefore, uptake by benthic algae is minimal, although we acknowledge that some remineralized nutrients could be taken up, at least temporarily, by sediment microbes.

To estimate the flux of nutrients through piscivores, we assumed that piscivore biomass was constant at the lake-wide scale. We assumed that piscivores assimilated 80% of the N and P they ingested from gizzard shad bodies, and therefore egested 20% of ingested N and P as feces (Schindler and Eby, 1997). We assumed that piscivore gross growth efficiency (N or P growth/N or P ingestion) was 30% for both N and P (based on Schindler and Eby, 1997). Therefore, piscivores excreted 50% of the N and P they consumed; this excretion was considered a source to the water column. Because we assumed that piscivore population biomass was constant, the production of piscivore carcasses was considered to be 30% of ingested N and P, i.e., equal to their growth at the population level. Thus, nutrients consumed by piscivores were allocated as follows: 20% egested as feces; 30% to mortality (piscivore carcasses), and 50% excreted as dissolved nutrients. N and P in piscivore carcasses was assumed to be mineralized at rates equal to those for adult gizzard shad carcasses. N and P egested by piscivores as feces was assumed to remineralize at the same rate as YOY gizzard shad carcasses, i.e., faster than adult shad or piscivore carcasses.

The modeling approach we employed for the fate of nutrients through piscivores is obviously a simplification, although assumptions about piscivory are based on data from Acton Lake. Nevertheless, we explored additional piscivory scenarios in which we relaxed these assumptions and compared these simulations to our "baseline" model. Specifically, we explored additional scenarios regarding our assumption that piscivore biomass was constant, and that piscivory accounted for 15% of mortality of gizzard shad $\leq$ 200 mm when temperature was $\geq$

10°. Data from Acton Lake show that piscivore catch-per-unit-effort declined in Acton Lake from 2003/2004 to about 2008, but no data are available before 2003 (**Supplemental Material**). We considered a scenario in which piscivore population biomass doubled from 1998 to 2003, from 20 to 40 kg wet mass/ha, to mirror the decline over the following 5 years. In addition, we explored scenarios in which we varied the percentage of shad mortality caused by piscivory, from 10 to 30% (see **Supplemental Material** for details), deviating from the baseline model in which it was 15%. In all scenarios, the flux of nutrients through piscivores was relatively small compared to that via non-piscivory gizzard shad mortality (see Results). Because the contribution of piscivores to the flux of nutrients was small, and for model simplification purposes, here we present the results that include the flux of nutrients through piscivory, i.e., piscivores excretion and mineralization from piscivores feces and carcasses, combined with non-piscivory gizzard shad mortality, i.e., carcass mineralization.

RESULTS

Remineralization rates of carcass nutrients (k) increased with temperature and were higher for YOY than adults (**Figures 2**, **3**, **Supplemental Table 2**). k was higher for N than P, reflecting the greater recalcitrance of P because of bones and scales. Q_{10} values for N and P ranged from ~1 to 3 depending on fish size and temperature increment (5–15 or 15–25°) (**Table 1**).

Over the 20-year period, 99.4% of the N and 98.6% of the P produced as gizzard shad carcasses were remineralized back to the water column. The dynamics of carcass production and remineralization followed a seasonal pattern and were strongly influenced by young-of-year fish (YOY), for both N and P (**Figure 4**). Nutrients accumulated in the carcass pool over winter months, when mortality was high and mineralization rates were low; in contrast, a net depletion of the carcass nutrient pool occurred during warmer months when mineralization rates were high. During July and August, a small peak in the carcass nutrient pool was also detected, due to a short-term accumulation of carcasses of YOY fish, followed by a rapid decrease until October (**Figure 4**). These dynamics reflect the high mortality rates, and rapid carcass mineralization rates, of YOY fish.

On an annual basis, N and P sequestered by the gizzard shad population via biomass production was higher than carcass mineralization in a few years, suggesting that fish biomass (living and dead) may act as a nutrient sink on a yearly time scale (**Figure 5**). However, in most years mineralization exceeded biomass production. Furthermore, for both N and P, excretion rates were higher (often much higher) than biomass production

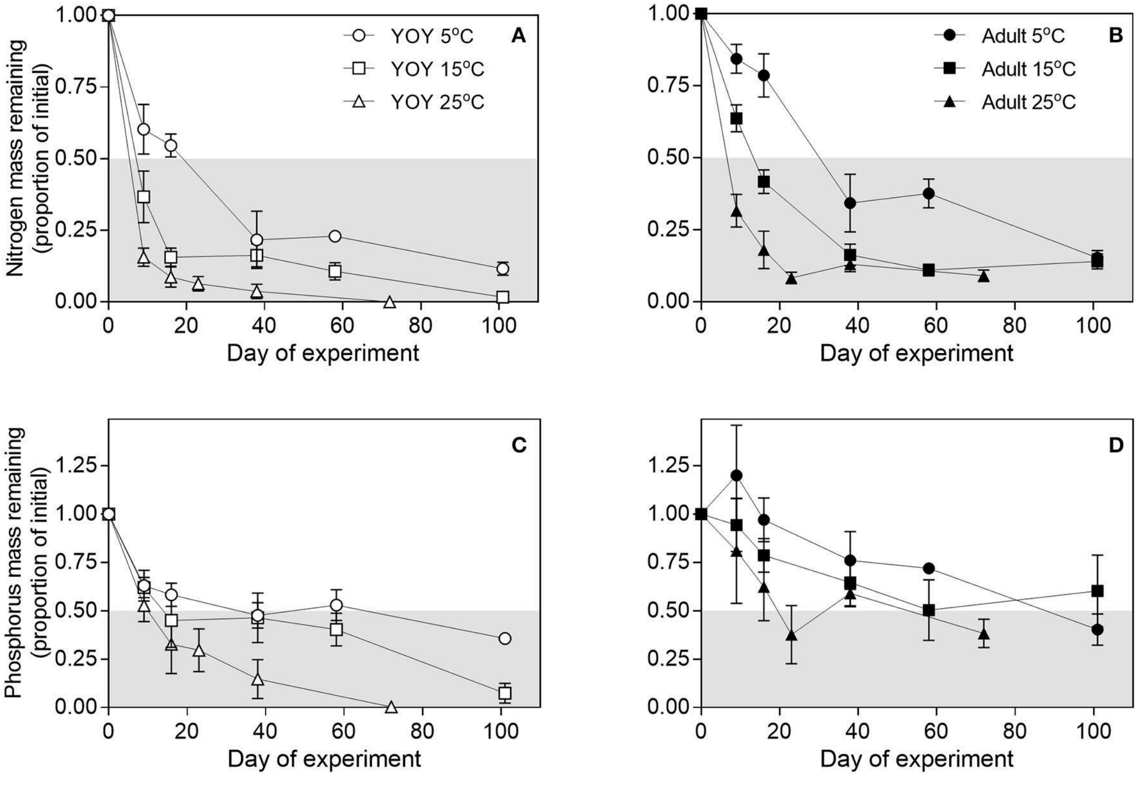

FIGURE 2 | Individual and interactive effects of fish size and temperature on patterns of mass remaining for **(A,B)** nitrogen **(C,D)** phosphorus mass in decomposing fish carcasses throughout time. Values are expressed as the proportion of initial mass in carcasses. Data for young-the-year (YOY) and adult fish are shown in separate panels for clarity. The transition between the white and gray areas in the panels indicate the half-lives of mass decay. Data points are mean ($n = 3$) and error bars are ± 1SEM.

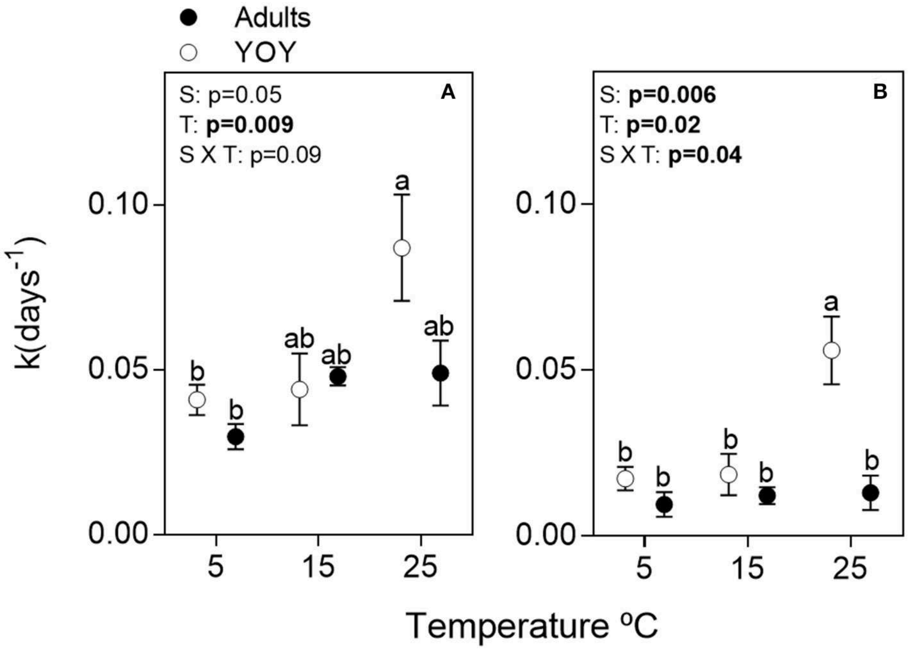

FIGURE 3 | Individual and interactive effects of fish size (S) and temperature (T) on time-integrated fish carcass decay coefficients (k) for **(A)** nitrogen and **(B)** phosphorus. Data points are means ($n = 3$) and error bars are ± 1SE. Different letters above treatments indicate significant statistical differences among treatments. Bold *p*-values depict significant statistical effects (Tukey's *pos-hoc* test; $p < 0.05$).

TABLE 1 | Q_{10} values for N and P decay rates through 38 days of the laboratory experiment.

Size class	Temperature range	Nitrogen	Phosphorus
YOY	5–15°	1.068	1.069
	15–25°	1.992	3.023
Adult	5–15°	1.606	1.278
	15–25°	1.020	1.074

Q_{10} values were calculated as the ratio between time-integrated fish carcass decaying coefficients (k) for each temperature level.

in all years (**Figure 5**). Thus, considering all fluxes, this fish population is a net source of N and P to the water column on an annual basis.

On a daily basis, the gizzard shad population was usually a source of nutrients. Thus, over the study period, mineralization plus excretion exceeded carcass production on 92.6 and 86.8% of days for N and P, respectively. The days on which nutrient accumulation in carcasses was higher than mineralization plus excretion occurred only during winter.

Piscivory accounted for the consumption of 15,133 and 4,037 g P/ha, representing, respectively, only 5.5 and 5.1% of total gizzard shad N and P biomass "lost" to total mortality. Over the 20-year period, almost all nutrients (99.9% of N and 99.7% of P) consumed by piscivores were released back to the water column via excretion, egestion, and piscivore carcass decomposition.

Results of the piscivory scenarios showed that the ultimate fates of nutrients from gizzard shad mortality were relatively insensitive to the assumptions in the baseline model. Doubling piscivore biomass from 1998 to 2003 reduced the flux of dissolved nutrients through piscivores (via piscivore carcass and feces mineralization, plus piscivore excretion) by 13% (N) or 15% (P) over this 5-year period, as these nutrients were stored in living piscivore biomass rather than mineralized (**Supplemental Material**). However, in total all of these fluxes through piscivores represent <6% of the flux via mineralization of gizzard shad carcasses; therefore, doubling piscivore biomass reduced total fluxes of N and P to the water column by <1% compared to the baseline model. Varying the percentage of gizzard shad mortality attributed to piscivores also had a relatively small effect on net N and P fluxes to the water column. As this percentage increased from 10 to 30%, N and P mineralization from the gizzard shad carcass pool declined, but this was accompanied by compensatory increases in piscivore excretion plus the mineralization of piscivore carcasses and feces (**Supplemental Figure 6**). In all scenarios, the percentage of nutrients produced via shad mortality that remained as carcasses (shad plus piscivores) was <0.6% for N and <1.4% for P. Thus, in all scenarios >99% of N and >98% of P were returned to the water column.

DISCUSSION

Our model suggests that, considering all fluxes of nutrients, this fish population is a net source of N and P to the water column, even though fish biomass is relatively high and fish are

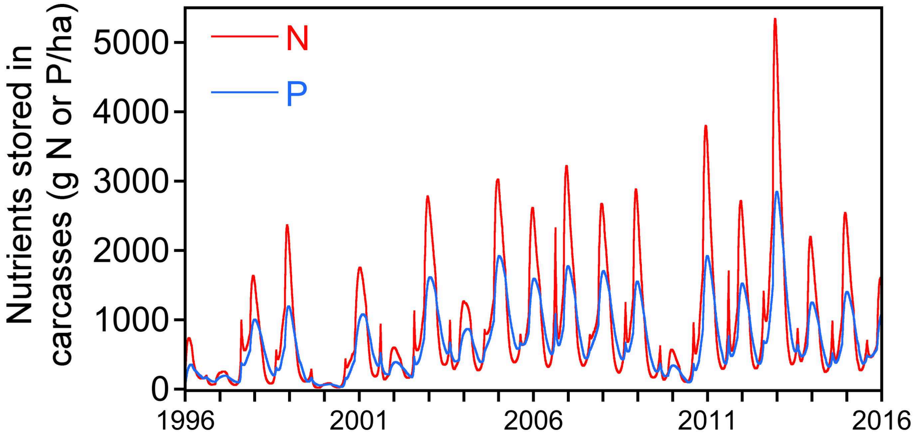

FIGURE 4 | Twenty-year time series showing the dynamics of phosphorus (blue line) and nitrogen (red line) stored in carcasses over time. The large peak occurring during winter is due to high mortality (high carcass production) rate of all age classes during this time, whereas the smaller peaks occurring in late July-August are due to production of carcasses from high mortality of young-of-year fish.

much more long-lived compared to phytoplankton, which are the dominant primary producers. In Acton Lake, phosphorus "trapped" in live gizzard shad biomass averaged about 47 μg P L^{-1} over our 20 year study, and lake "total P" (P in the water column, excluding fish) averaged about 105 μg P L^{-1} Therefore, the gizzard shad population contains a pool of P equal to roughly 45% of the traditionally-measured "total P." However, almost all of this P becomes available relatively quickly after fish die and decompose. Thus, neither the high biomass of living fish nor the production of carcasses renders this population a long-term nutrient sink.

The rate at which nutrients are remineralized from fish carcasses is likely to vary greatly among ecosystems. Boros et al. (2015) argued that fish carcasses are not likely to act as a long-term P sink in warm-temperate shallow lakes. In their experimental work, carcasses of gizzard shad and bluegill (*Lepomis macrochirus*) decomposed completely over ∼3 months in mesocosms that were warm (mean temperature 24.5°C) and well oxygenated, i.e., conditions similar to those in Acton Lake in summer. Thus, Acton Lake has conditions that are favorable for carcass decomposition. In deeper, colder lakes fish carcasses may be nutrient sinks (Kitchell et al., 1975; Parmenter and Lamarra, 1991), but much depends on carcass remineralization rates. Parmenter and Lamarra (1991) studied carcass decomposition of rainbow trout (*Oncorhynchus mykiss*) in colder environments (2–5°C) and found that most of the decomposition activity took place during the initial 60 days of carcass decomposition. By the end of the experiment fish carrion lost 95% of original carcass N, but only 60% of carcass P due to its presence in more recalcitrant tissues. Chidami and Amyot (2008) argued that water temperature can be used as a surrogate for decomposition rates in freshwaters. Studying boreal lakes, they found that decreasing temperatures are related to increased decomposition half-lives, probably due to lower metabolic activity of decomposing bacteria and scavengers.

Animal size also plays a role. We found that remineralization rates were higher for small gizzard shad carcasses than for large carcasses, although all sizes decomposed rapidly at warm temperatures. Very large animal carcasses will probably decompose even more slowly; for example, Subalusky et al. (2017) found that wildebeest bones take 7 years to fully decompose even in a warm, tropical river. In ecosystems where bones mineralize slowly, carcasses are more likely to be long-term sinks for P, than for N.

In our model, carcasses mineralized fairly rapidly, so at an annual scale they were not a sink for nutrients. However, because of variation in water temperature and fish size, we found temporal variation in the amount of nutrients being stored in vs. mineralized from carcasses, at annual and seasonal scales. Thus, while the population is a net source of N and P to the water column, there are specific periods when N and P accumulate in live biomass or in carcasses, and during these periods the population acts as a temporary sink. During winter, for example, both excretion and decomposition rates are low, promoting a short-term nutrient accumulation in fish carcasses. In terms of fish population biomass, short term sinks also occur in summer during the period of YOY growth followed by higher rates of YOY mortality. The strong influence of the YOY on the dynamics of carcass production and N and P remineralization (**Supplemental Figure 4**) is due to the variability in the number of fish born across years (Kraft, 1992; Williamson et al., 2018), the high mortality rates of this age class, and the fact that YOY carcasses decompose rapidly. However, during these periods excretion rates are high and exceed this potential sink. These dynamics illustrate the importance of explicitly considering both temporal scale and the multiplicity of potential fluxes of nutrients when analyzing the extent to which fish are sources or sinks of nutrients.

It is potentially informative to compare nutrient fluxes from our model with other fluxes from sediments to water. Nowlin

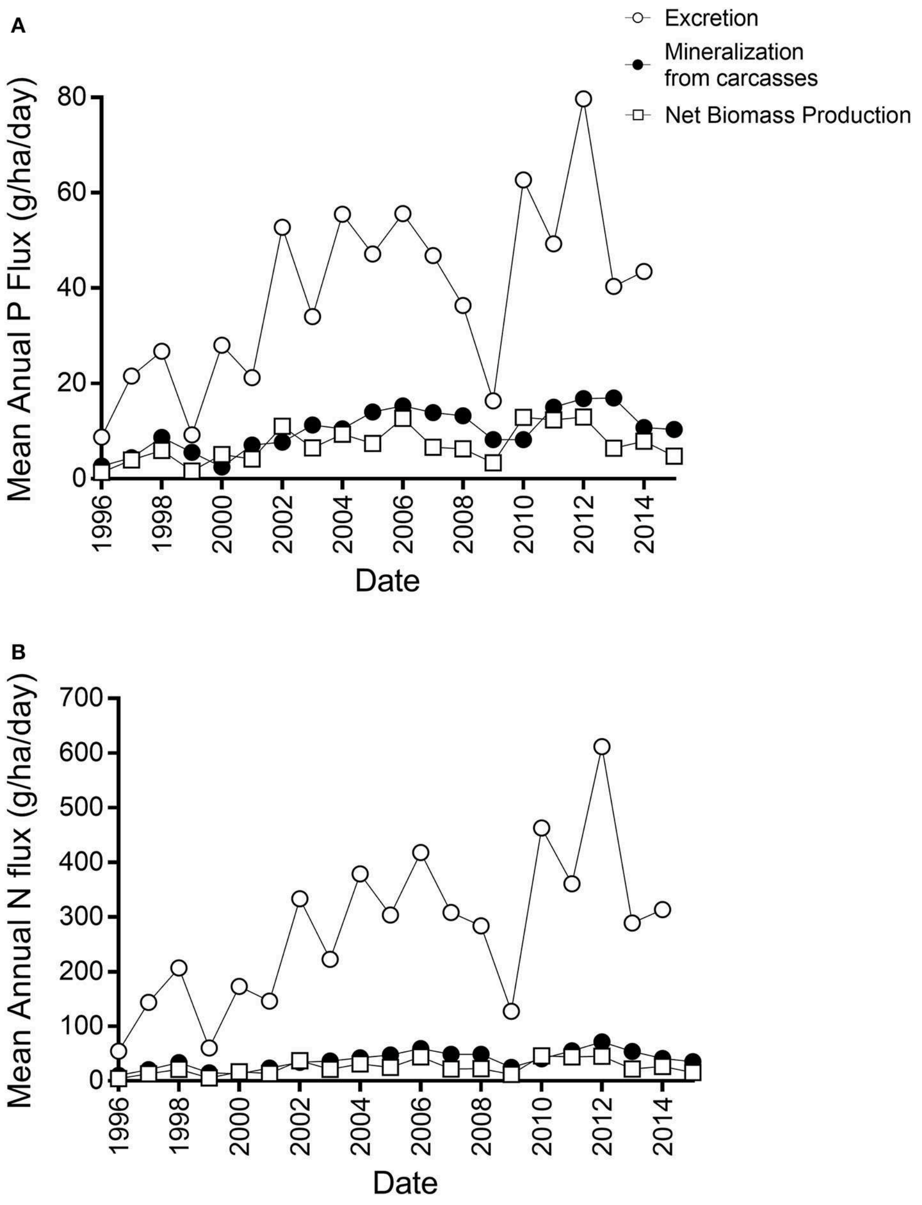

FIGURE 5 | Annual fluxes of phosphorus **(A)** and nitrogen **(B)** for net biomass production (white square), carcass remineralization (black dots), and excretion (white dots).

et al. (2005) measured N and P fluxes from Acton Lake sediments using sediment core incubations; these "direct" fluxes are probably mediated mainly by microbes but also may include excretion by small invertebrates that happen to be in the cores. In summer (the only period when core incubations were done), direct fluxes of NH_4 exceed carcass N mineralization by 4-5X at the lake-wide scale (**Table 2**). For P, the results are more complex. As would be expected, direct flux of P is much higher (>9X) from anoxic, hypolimnetic sediments than from oxic sediments; the mineralization rate of P from carcasses is similar in magnitude to direct flux of P from oxic sediments (**Table 2**). At a lake-wide scale, accounting for the areas of oxic and anoxic sediments, direct P flux exceeds carcass mineralization by 4-5X. However, Nowlin et al. (2005) showed that very little of the P released from hypolimnetic sediments is transported to the euphotic zone where phytoplankton can use the P, probably because P precipitates with calcium in the hypolimnion and sinks to sediments. Regardless of the relative magnitudes of direct fluxes vs. carcass mineralization rates, it is clear from our study that carcasses do not represent long-term sinks. Furthermore, during summer, excretion by gizzard shad exceeds direct fluxes from sediments for both N and P (**Table 2**).

Our study is unique in that we have extensive data on the fish population dynamics (including all age classes) at the

TABLE 2 | Comparison of different fluxes from sediments to water in Acton Lake.

	Mean N flux (g N ha^{-1} d^{-1})		Mean P flux (g P ha^{-1} d^{-1})	
Nutrient source	**Summer**	**Annual**	**Summer**	**Annual**
Excretion by gizzard shad	622.0	262.3	97.1	37.7
Mineralization of gizzard shad carcasses	31.5	35.7	8.4	10.2
Direct flux from sediments				
Outflow site (anoxic, hypolimnion)	194.0		91.1	
Inflow site (oxic, unstratified)	117.6		9.8	
Lake-wide (weighted average)	144.3		38.2	

*Summer values are those from July through September, and annual values are over the entire year. Excretion data are taken from Williamson et al. (2018); the "annual" mean presented here is the mean of the points in **Figure 5**. Direct flux data are taken from Nowlin et al. (2005) and are based on data from summer 1996, the only time period for which we have experimental data. Fluxes were measured by incubating sediment cores from two sites, an Inflow ("River") site where depth is ∼1 m and the water column is always well-mixed and oxic, and an Outflow ("Dam") site where sediments were taken from the anoxic hypolimnion. Details are provided in Nowlin et al. (2005). The lake-wide direct flux value was obtained as a weighted mean assuming that anoxic and oxic sediments comprise 35 and 65% of the lake bottom, respectively.*

ecosystem level and over a 20-year period. This large and comprehensive dataset allowed us to produce robust estimates for population dynamics as well as fluxes of nutrients mediated by the population. With the exception of research on Pacific salmon (e.g., Tiegs et al., 2011; Rüegg et al., 2014), the fate of carcasses in freshwater environments has not been explored as much as in marine and terrestrial systems (Beasley et al., 2012), so our study helps to fill this gap in the nutrient cycling literature. We encourage additional whole-ecosystem studies that assess whether animals are nutrient sources or sinks. The fates of nutrients associated with different mortality sources need to be explored more (Barton et al., 2019). Based on our results, nutrients consumed by fish piscivores are not likely to be long-term sinks. However, piscivorous birds may function as sinks by transporting nutrients away from an aquatic ecosystem. In addition, the role of scavengers in processing carcass nutrients needs to be evaluated. More broadly, to fully understand the role of animals as nutrient sources or sinks, we need studies in a range of environments that reflects the breath of variation in habitat features such as depth, temperature, the balance of benthic vs. pelagic production, and other potential drivers.

ETHICS STATEMENT

This study was carried out in accordance with the recommendations of the Miami University Institutional Animal Care and Use Committee.

AUTHOR CONTRIBUTIONS

RN and MV conceived the population model. LC and SP conducted the lab experiments. MG and MV collected the data on the fish population. RN, MV, and LC wrote the final versions of the manuscript. All authors contributed to writing the paper.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2019.00340/full#supplementary-material

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

FINAL CONSIDERATIONS

Alterations of global nutrients cycles leading to impaired water quality and biodiversity loss are two main problems that we are facing as we advance on the Anthropocene, the new epoch dominated by human induced changes on natural ecosystems. Recognized leading causes of this threats are habitat degradation caused by conversion of natural areas to human land use (e.g. farming, urbanization) and climate change. However, the interactions of land use with climatic and morphometric characteristics of the habitat are still not well understood, especially in lentic tropical freshwaters. In this thesis we aimed to address this gap by exploring the individual and interactive effects of land use (i.e. type, proximity and extent) landscape properties (i.e. lake origin, lake and catchment absolute and relative size and geomorphology) and precipitation on water quality indicators and on local and regional taxonomic phytoplankton diversity in 98 lakes located in Rio Grande do Norte, northeast Brazil (Chapters one and two).

On chapter one, our goal was to evaluate the effects of landscape properties (morphometric measurements of lakes and their catchments), precipitation patterns, and land use properties (extent and proximity of the land use to water bodies) on water quality of the 98 studied lakes in northeast Brazil. In our study, we used a Principal Component Analysis (PCA) incorporating parameters correlated with eutrophication including nitrogen (N), phosphorus (P) and Chlorophyll-a to extract a composite response variable representing water quality impairment (WQI). After that, we used a Regression Tree Analysis (RTA) to study the influence of land use, landscape properties and precipitation on this composite variable. Overall, results from the RTA suggested that WQI was related to highly impacted buffer zones, and this effect of land use is intensified by high variability in precipitation. High BA:Vol was also a relevant parameter for ecosystems with less impacted buffer zones. These results indicate that ecosystems subjected to intense episodic rain events (e.g.

storms) and higher buffer areas relative to aquatic ecosystem size (i.e. small waterbodies) are more susceptible to impacts of land use. The proportion of land use at the catchment scale was also important for the largest water bodies. Given our findings, we conclude that spatial and climatic information are needed to understand land use effects on water quality. Thus, to better manage water quality, it is necessary to consider an integrative approach, which includes watershed management within the context of climate change.

In chapter two, we characterized the 98 lakes as natural or artificial and compared them regarding the landscape properties of their surroundings, their morphometry, and their physico/chemical characteristics to verify whether those factors can be associated with average patterns of phytoplankton community structure at both local and regional scales. We observed substantial differences among lakes and reservoirs, with reservoirs presenting, on average, morphometric and landscape characteristics that make them more suitable to higher inputs of allochthonous material entering the system. Reservoirs were also more productive (in terms of nutrients and Chl-*a* concentrations), however these higher eutrophic conditions were not associated with total phytoplankton biomass, neither with local diversity patterns (i.e. species richness, evenness and Simpson's diversity). We observed that reservoirs are important systems promoting phytoplankton diversity as they had higher gamma diversity, probably due to the higher number of exclusive species. This importance is enhanced when we analyze both lakes and reservoirs system combined as they held a greater regional species richness than the two types of ecosystems alone. This finding suggests that complementarity in species composition among these two types of ecosystems is a fundamental factor to the large-scale patterns in phytoplankton diversity. Thus, we recommend that freshwater managers and policy makers must include scenarios with a combination of lakes and reservoirs in the landscape in order to preserve phytoplankton biodiversity in a regional scale.

Additionally, because nutrients balance in freshwater systems can also be affected by a variety of internal processes such as nutrients translocations by fish and carcass decomposition, we explored a second framework in chapter 3, which is a long-term temporal framework focused on internal processes related to nutrient cycling where we assessed whether an omnivorous fish (*Dorosoma cepedianum*) with high biomass and growth rate is a source or sink of N and P to the pelagic zone of a temperate eutrophic lake, at various time scales ranging from days to 20 year. In brief, we found that remineralization rates of P and N allocated in fish carcasses increased with temperature and decreased with fish size. Over the 20 years ~ 99% of all N and P produces as fish carcasses were remineralized back to the water column, suggesting that fish carcasses are not a long-term sink of nutrients to this compartment of freshwater systems. When analyzing data annually, we found that in some years the biomass production was higher than mineralization, however nutrient excretion by the population greatly exceeded sequestration of nutrients in biomass (living and dead) in all years. From this study we conclude that the population of *Dorosoma cepedianum* is a significant net source of nutrients to the pelagic habitat on the lake-wide scale. Our population model shows the importance of considering spatial and temporal scale as well as long-term population dynamics when studying the role of animals as nutrient sources or sinks.

APPENDIX

Appendix A. Supplemental material of chapter 1

PRECIPITATION, LANDSCAPE PROPERTIES AND LAND USE INTERACTIVELY AFFECT WATER QUALITY OF TROPICAL FRESHWATERS

1. *Delineation of catchment areas*

Aiming to analyze the extent of the impacts of land use on water bodies, catchment areas and 100 meters buffer zones were delineated for each lake. To delineate catchments, a 30 m Digital elevation model (DEM) mosaic comprising the states of Rio Grande do Norte and Paraiba was gathered from Brazilian Geomorphometric database (TOPODATA) available at http://www.dsr.inpe.br/topodata/acesso.php. Fill sinks function was used as a DEM manipulation procedure in order to fill any existing depressions in the DEM file that could obstruct water flow. Delineation of catchments was based on lakes polygon shapefiles and it was performed using ArcHydro 2.0 Toolbox (ArcHydro, 2011) on ArcGis 10.5.1 (ESRI, 2017).

2. *Lake morphometry – Estimations of catchment and buffer slopes and lake volume*

2.1- Slope

We measured the slopes of catchment and buffer areas for each lake. We extracted slopes from a 30-m digital elevation model (DEM) comprising the state of Rio Grande do Norte using the slope function at ARCMAP software. Data was gathered from the Brazilian Geomorphometric database (TOPODATA), available at http://www.dsr.inpe.br/topodata/acesso.php. However, because the region studied is mostly flat, average slope of all catchments did not present a lot of variation (mean and SD; $2.1^{o} \pm 1.24^{o}$) and we decided to not include this data in the models.

2.2 - Lake volume

Lake volume was calculated through the hyperbolic function 0.43 × lake area × depth (Post et al., 2000). In our study we decided to use lake volume in all ratios to have a more proximate estimation on the variability of ecosystem size among lakes and reservoirs, harder than lake surface area alone. Although the ideal methodological approach to obtain lake volume measurements would be to conduct bathymetric surveys, it would be expensive and time consuming. As demonstrated by Cael et al. (2016), volume-area scaling based on the Hurst coefficient is an accurate and consistent method for lake volume estimates when applied to lake data sets globally. Additionally, according to Messager et al. (2016) the depth of lakes is generally reflected by the slope of their immediate surroundings. Overall, the landscape in our studied region is mostly flat with average slopes of 1.97^o on the buffer zones of the lakes (range: min = 0.31^o; max= 4.36^o), thus we believe that our depth measurements on the central portion of the lakes gives a good proxy of lake depth to estimate lake volume. We compared our volume estimates calculated with the hyperbolic function 0.43 × lake area × depth proposed by Post et al. (2000), with the area-scaling relationship proposed by Cael et al. (2016) (equation 1) and they were significantly correlated (Pearson's $r^2 = 0.73$; Figure S1).

3. *Computation of precipitation magnitude and variability for each lake*

The studied area is known for presenting a latitudinal gradient in precipitation, going from higher precipitation on the coastal region (tropical humid and tropical semi-humid climatic subdomains; annual precipitation ~800-1200mm) to less precipitation on the semi-arid region which is embedded in the semiarid climatic subdomain with annual precipitation ranging from ~400 – 800mm (Diniz and Pereira 2015;INMET 2015; Cabral et al. 2019).

In order to calculate the magnitude and the temporal variability of precipitation we used, respectively, the cumulative monthly precipitation and the coefficient of variation of monthly precipitation data from September 2010 to September 2012 (Source: INMET Instituto Nacional de Meteorologia) This data was available for seven meteorological stations (pij) located at the state of Rio Grande do Norte. To obtain the magnitude ($Pj\ Tot_{precip}$) and variability ($Pj\ CV_{precip}$) of precipitations for each lake, the weighted average of the values for the seven different stations was computed, with weights (Wij) proportional to the distance between the lake and the stations (dab) as follows:

Eq.(A.1)

$$Pj = \sum_{i}^{7} Wijpi$$

and,

Eq.(A.2)

$$Wij = \frac{dij^{-1}}{\sum_{k}^{7} dkj^{-1}}$$

Where,

Pj = precipitation magnitude or variability measured at lake j

pi = precipitation magnitude or variability measured at station i

dab = distance between lakes a and station b.

Distance between lakes and stations where calculated using the haversine formula.

We compared the precipitation values we obtained from interpolation for each lake, with the values obtained from the long-term (1970-2000) Worldclim database. We found that the values of average monthly precipitation obtained from the Worldclim database (https://www.worldclim.org/) are very similar to the ones we obtained with the interpolation method using the INMET weather stations as we saw a strong correlation among the two datasets (R^2=0.61; Figure S2).

4. Statistical Analysis

To verify the relationships among climate, land use and landscape properties on the water quality, regression tree analysis (RTA) were performed using the rpart package in R (Breiman et al., 1984). RTA is non-parametric statistical technique that allows one to explain the variation of a single response variable by one or more explanatory variables (DE'ath & Fabricius, 2000). Trees are constructed by recursively partitioning the data with binary splits. Each split is done envisioning to maximize the homogeneity of the resulting groups, based on the response variable, while producing a tree with a reasonable small size and interpretable value (DE'ath and Fabricius, 2000; Prasad et al., 2006). To build a RT, two important parameters must be selected: the minimum number of splits (minsplit) and the complexity parameter (cp). They both define constraints on the way the rpart package can create the tree: a split can only be attempted if both resulting nodes contain at least minsplit datapoints and if the lack of fit of the overall tree is decreased by at least cp – the lack of fit being defined by the chosen optimization method, in our case ANOVA. Given the minsplit parameter, the rpart package proposes an automatic procedure to optimize cp through 10-fold cross-validation on the dataset. However, the choice of minsplit is left to the user. To choose an optimal minsplit we propose a cross-validation based methodology. Cross validation is a method coming from machine learning which can be used for parameter selection. It consists in splitting the dataset in two (training set and test set), the training set is used to fit the model with a given set of hyperparameters (minsplit in our case) and the test set to evaluate it. Because the test set was not provided to the RT during training, if the predictions on the test set are good, it means that the chosen hyperparameters did not overfit the data presented and that the model is likely to generalize well to unseen data. For machine learning standards, the size of our dataset is rather small and for this reason, we choose to apply leave-one-out cross validation (LOOCV) to choose minsplit. If our dataset contains n data points, LOOCV consists in building training set of n-1 points and testing set of size 1. The score of a given minsplit is obtained by averaging the cross-validation RMSE after training N trees (each datapoint is left one time in the test set). We run our LOOCV code for different values of minsplit and retain the one with the lowest cross-validation RMSE score. This way, we can ensure that the chosen minsplit-cp pair is the one that generalizes better for the kind of lakes studied. In the result section, we report the R2 and RMSE values.

Figures

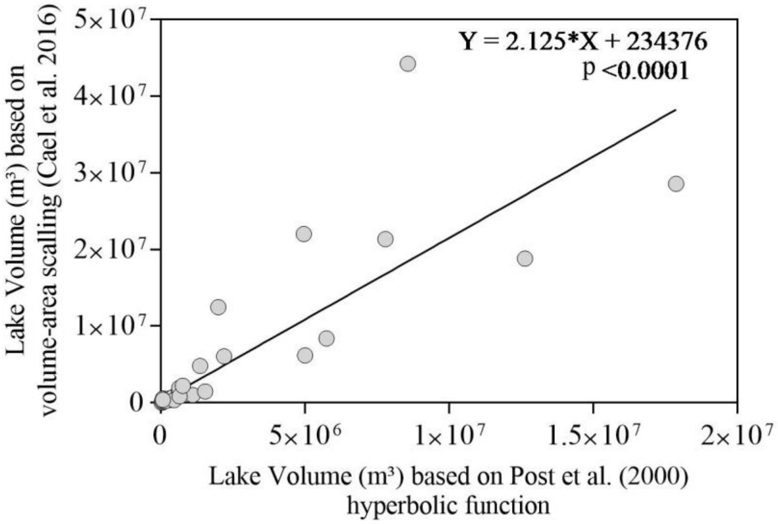

Fig. S1 – Linear regression of lake volume based on volume-area scaling relationship as proposed by Cael et al. (2016) and estimation of lake volume based on Post et al. (2000) hyperbolic function

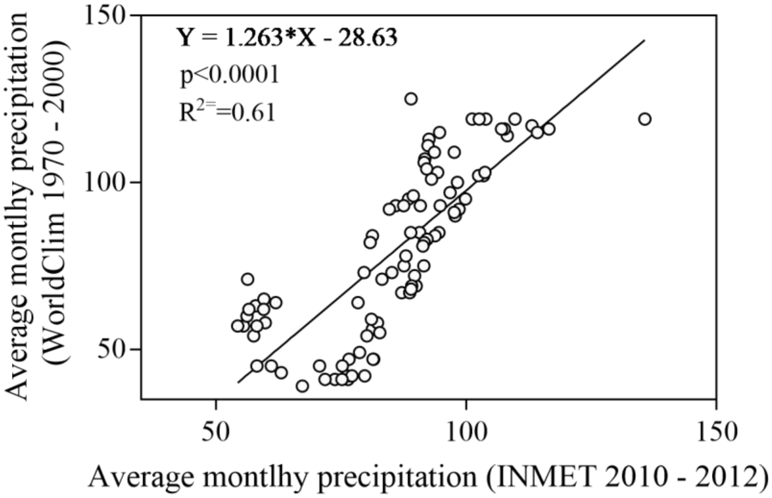

Fig. S2 – Linear regression of precipitation data obtained from Wordclim database and from INMET weather stations interpolation.

Tables

Table S1 – Statistical results from PCA showing the eigenvalues, percentage of variance explained and broken-stick distribution to evaluate significance of PCA axis.

	Axis 1	Axis 2	Axis 3
Eigenvalue	1.98	0.59	0.42
Percentage of variance	66.01	19.87	14.11
Broken-stick percentage	61.11	27.77	11.11

Table S2 – Variance inflation factor (VIF) for the main explanatory variables studied.

Variables	Tot_{precip}	Cv_{precip}	LP:VOL	CA:VOL	BA:VOL	Ant_{CA}	Ant_{BA}
VIF	4.64	4.27	8.82	1.72	8.95	1.91	1.77

Tot_{precip}: magnitude of precipitation; CV_{precip}: variability of precipitation; LP:Vol: lake perimenter to lake volume ratio; CA:Vol: catchment area to lake volume ratio; BA:Vol: buffer area to lake volume ratio; Ant_{CA}: proportion of anthropogenic land use on the catchment area; Ant_{BA}: proportion of anthropogenic land use on the buffer area

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Appendix B. Supplemental material of chapter 3

This Supplementary Material can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2019.00340/full#supplementary-material

FISH, INCLUDING THEIR CARCASSES, ARE NET NUTRIENT SOURCES TO THE WATER COLUMN OF A EUTROPHIC LAKE

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Laboratory experiment to measure fish carcass decomposition rates

Methods

We conducted a laboratory experiment to evaluate the individual and interactive effects of fish size and water temperature on loss of total dry mass and body tissue C, N and P mass from decomposing fish carcasses. Carcasses of gizzard shad (*Dorosoma cepedianum*) of two size classes [young-of-year (YOY) and adult fish - see table S1] were orthogonally manipulated over three water temperatures (5 °C, 15 °C and 25 °C). The water temperature range encompasses most of the variation in water temperature in Acton Lake throughout the year. Each of the six treatments was replicated 15 times but 3 replicates were sacrificed on each of 5 sampling dates during the experiment. Therefore, the total experimental design consisted of 90 replicates (i.e., 2 fish sizes × 3 temperatures × 5 sampling dates × 3 replicates). The fish used in the experiment were captured from Acton Lake via electrofishing one day before the start of the experiment. The individuals were immediately euthanized and kept at constant cool temperature (~ 4 °C) until the start of the experiment. Adult individuals of gizzard shad may vary in size relative to the size we used in the experiment [1]. However, a pilot experiment conducted at Acton Lake found that the decomposition of gizzard shad carcasses did not differ significantly between two disparate sizes of adult fish. Therefore, we opted to use the size class representative of adult fish that is more abundant, and representative of adult gizzard shad individuals in Acton Lake.

The experiment was performed in small aquariums (hereafter microcosms) with a volume of approximately 3L (10 cm height × 30 cm length × 10 cm width). Each microcosm received a sediment layer and an overlaying water column of approximately 2-cm and 6-cm deep, respectively. Both sediment and water used in the experiment were collected from Acton Lake. To remove macrofauna and to guarantee homogeneity in the starting conditions among experimental microcosms we homogenized and sieved the sediment before placing it in the microcosms. Each individual microcosm received one fish, either an adult or YOY gizzard shad (mean wet mass ± SD: 55 g ± 5.2 and 12 g ± 1.1, respectively). Initial values for dry mass as well as C, N and P mass contained in each microcosm can be seen in table S1. Water temperature was manipulated by distributing microcosms across 3 growth chambers, each one adjusted to a given temperature. Because the environmental conditions may vary slightly along the shelves within the growth chamber, we distributed time replicates for the two fish sizes (i.e. 2 size classes × 5 sampling dates) across 3 shelves within each growth chamber (ten microcosms per shelve). Therefore, shelves were considered as experimental blocks.

Experimental duration as well as the time interval between the sampling dates were different for the warmest temperature. The 5 °C and 15 °C treatments were sampled at 9, 16, 38, 58 and 101 days after the beginning of the experiment. The 25 °C treatment was sampled at 9, 11, 18, 38 and 72 days after the beginning of the experiment. The experimental duration and sampling intervals differed for the 25°C treatment because we observed that carcass decomposition was faster in this treatment. However, the experimental duration is well within that of other studies evaluating fish carcass decomposition [2, 3]. To keep microcosms oxygenated throughout the experiment, each microcosm was aerated constantly and kept in the dark. Every 3 days, we replaced the water evaporated from each microcosm by the addition of a same volume of deionized water. To estimate fish dry mass as well as C, N and P mass in each microcosm at the beginning of the experiment, we weighed 20 individuals of each size class (to the nearest 0.0001 g) to obtain the mean wet carcass mass. Then we placed fish carcasses in a drying oven at 60 ^{o}C until they reached constant dry mass. Finally, we calculated a dry:wet mass ratio and used it to estimate the initial dry mass in each microcosm.

On each sampling date, 3 replicates from each treatment were sacrificed. Carcasses were carefully separated from sediment particles and immediately dried at 60 ^{o}C until reaching constant mass. Then the dry mass of the remaining fish carcass from each microcosm was estimated. Carcasses from each microcosm as well as those used for initial dry mass estimation were analyzed for C, N and P concentrations. Carcasses were ground to powder using a mortar and pestle. However, fish carcasses used to estimate initial body C, N and P concentrations were gutted before analysis to avoid contamination from ingested food for estimates of carcass elemental composition. Body C and N contents were obtained with a CHN analyzer, and P content was measured as soluble reactive P with an autoanalyzer following digestion of tissue with HCl[4].

Proportion dry mass remaining was expressed as the dry mass of a carcass at a given sampling date divided by initial dry mass. To estimate C, N and P masses in carcasses, the dry mass of each carcass was multiplied by the C, N and P contents (proportion of dry mass) for each carcass. Then the elemental mass of each carcass (g C, N or P per carcass) was divided by the mean initial elemental mass at the beginning of the experiment.

Supplemental Table 1. Initial values for adult and young-of-year (YOY) carcasses used in the experiment. Len = total length (mm); Wet mass (g.ind^{-1}); iC, iN and iP are initial carbon, nitrogen and phosphorus concentrations (% of dry mass), respectively; and iMass, iCm, iNm and iPm are initial total carcass dry mass, carbon, nitrogen and phosphorus masses (g per carcass). Values are mean and standard deviations (in parentheses). Values of iC, iN and iP were analyzed using gutted fish.

	Len	Wet mass	iMass	iC	iN	iP	iCm	iNm	iPm
Adult fish	188.9	55.9	12.3	49.3	9.1	3.6	5.83	1.08	0.44
	(4.25)	(5.24)	(1.15)	(3.49)	(0.89)	(0.22)	(0.50)	(0.11)	(0.09)
YOY	41.3	4.3	0.94	40.1	12.1	2.6	0.39	0.11	0.02
	(1.23)	(0.72)	(0.16)	(0.61)	(0.19)	(0.73)	(0.06)	(0.02)	(0.005)

Because experimental duration and sampling intervals differed between the 25 ^{o}C treatment and the other two treatments, we did not compare the effects of fish size and temperature on fish carcass decay rates for each sampling date. Instead, we chose to calculate a global decay constant (k) as a time integrated measure over the time. We calculated the k (days^{-1}) considering the experimental duration of 38 days, because decomposition rates were monitored for all experimental treatments within this time period. For each response variable, three k-values (one for each block/growth chamber shelves) were calculated for each fish size-temperature treatment combination. The k-values for each response variable were calculated as the linear coefficient of the correlation between the log-transformed values of dry and nutrient mass remaining and time (i.e., 38 days), i.e., $k = (\ln(M_{38}/M_0))/38$. Finally, we used Q_{10} as a standardized measurement to evaluate the magnitude of effects of temperature on decay rates for each fish size class. To better evaluate the effect of temperature changes on fish carcass decomposition rates, Q_{10} was measured for the decay rates (k) for dry mass, C, N and P for both temperature intervals, 5 ^{o}C to 15 ^{o}C and 15 ^{o}C to 25 ^{o}C. Q_{10} was calculated as (k_{15}/k_5) and (k_{25}/k_{15}) for the first and second temperature intervals, respectively, where k_5, k_{15}, and k_{25} are the decomposition rates along 38 days at 5 ^{o}C, 15 ^{o}C and 25 °C. Analysis of variance were performed using the software STATISTICA, version 7.0 (Statsoft, Inc). A significance level of □=0.05 was considered for all statistical analysis.

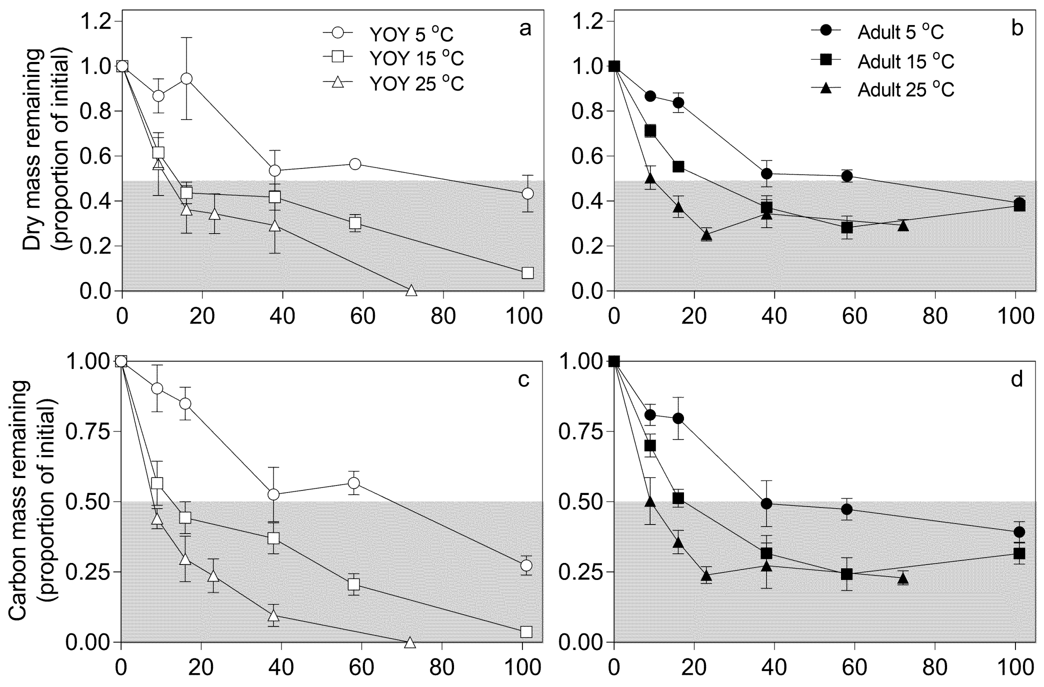
Results

In general, the decay rates for dry mass and the three elements differed in their responses to experimental factor manipulated. There were no significant individual or interactive effects of fish size or temperature on k for carcass dry mass through 38 days of experimental duration (Figures S1 and S2 and Table S2). However, inspection of Figure S1a suggests that k could be quite different between YOY and adult fish if we compared their dry mass decay for longer time periods. Carbon k was significantly affected by temperature and its interaction with fish size (Table S2). Fish carcasses lost C mass faster at the highest temperature but only for YOY fish (Figure S1). As stated in the main text, temperature had a significant effect on k for both N and P, and fish size had a significant effect on k for P and a marginally significant effect on k for N (Table S2).

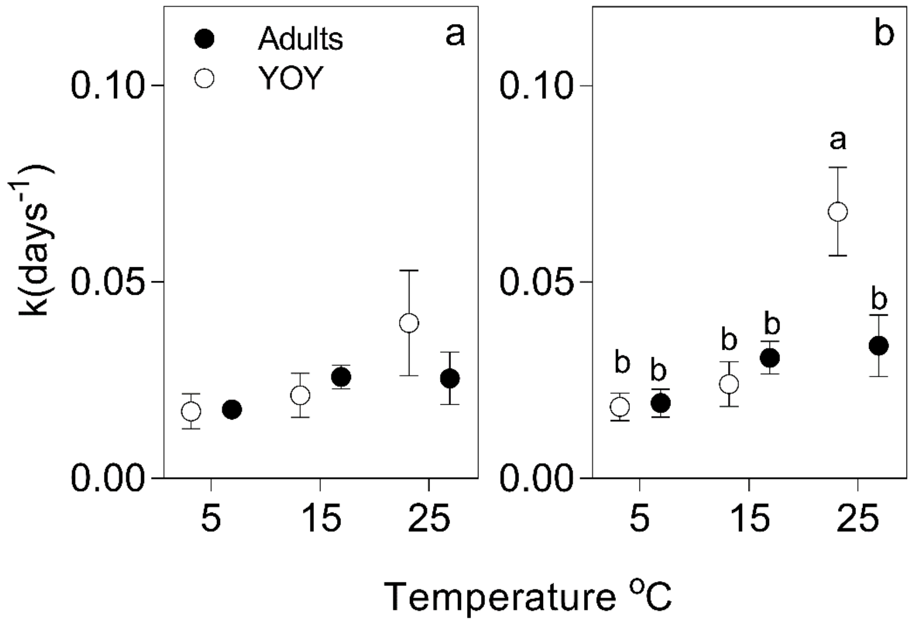
Q_{10} values for decay rates (k values) of YOY and adult fish were quite similar for all response variables for the 5-15 ^{o}C temperature range (Figure S3). However, Q_{10} values for YOY decay rates were higher than those for adult fish at the 15-25 ^{o}C temperature range for all response variables but especially for C, where Q_{10} values for YOY were almost 3 times higher than those of adult fish. Also, in general, Q_{10} values tended to be lower for adult carcasses than for YOY carcasses over the warmer temperature range (15-25°C). However, the opposite pattern is observed for YOY carcass decomposition, where Q_{10} values tend to increase somewhat at the warmer temperature range.

Supplemental Table 2. Summary of the two-way factorial analysis of variance depicting the statistical results for the individual and interactive effects of fish size and temperature on the average k value (i.e. linear constant of decay) for the four response variables analyzed. Bold p-values depict significant statistical effects. df = degrees of freedom; MS = mean of squares.

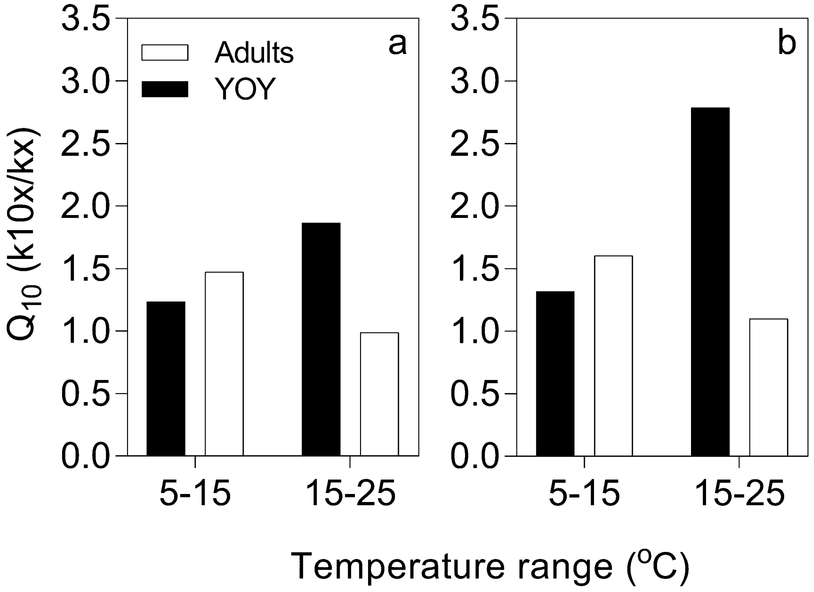
Response variable	Factor	df	MS	F	P
Dry mass remaining	Fish size (S)	1	0.00004	0.18	0.67
	Temperature (T)	2	0.0003	1.62	0.23
	S × T	2	0.0001	0.66	0.53
	Error	12	0.0002		
Carbon mass remaining	Fish size (S)	1	0.0003	1.37	0.26
	Temperature (T)	2	0.0016	6.53	**0.01**
	S × T	2	0.0007	2.88	**0.04**
	Error	12	0.0002		
Nitrogen mass remaining	Fish size (S)	1	0.001	4.39	0.05
	Temperature (T)	2	0.0016	7.01	**0.009**
	S × T	2	0.0006	2.92	0.09
	Error	12	0.0002		
Phosphorus mass remaining	Fish size (S)	1	0.0016	10.68	**0.006**
	Temperature (T)	2	0.0008	5.34	**0.02**
	S × T	2	0.0006	4.21	**0.04**
	Error	12	0.0002		



Supplemental Figure S1. Individual and interactive effects of fish size and temperature on patterns of mass remaining for (a-b) dry mass and (c-d) carbon mass (d-e) in decomposing fish carcasses throughout the time. Fish carcass mass remaining was estimated as the proportion of initial mass. Data for young-of-year (YOY) and adult fish are shown in separate panels for clarity. The transition between the white and grey areas in the panels indicate the half-lives of mass decay. Data points are mean (n=3) and error bars are ± 1SEM. Trends for carcass N and P are presented in Fig. 2 in the main text.



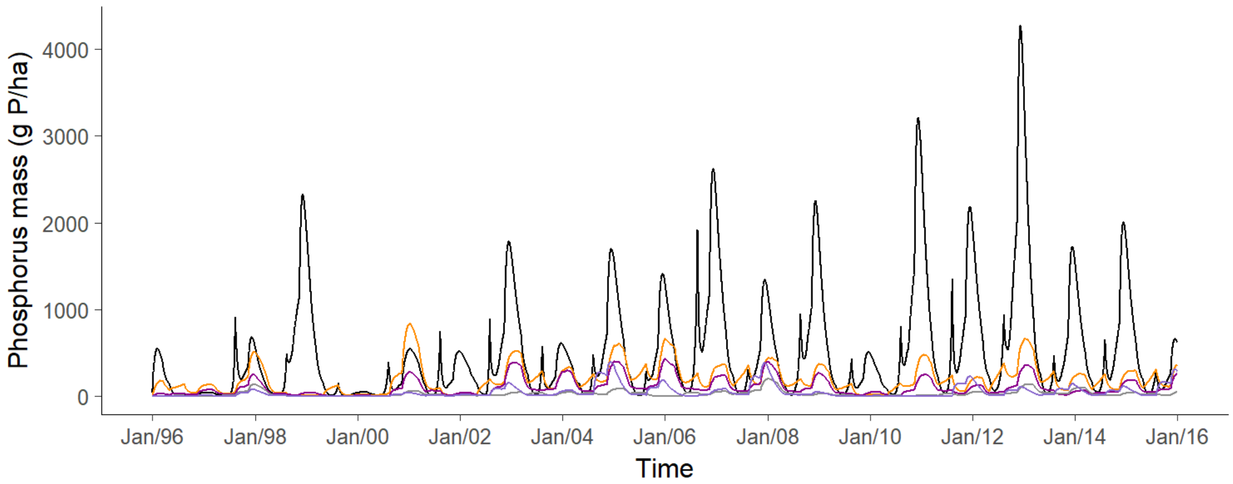
Supplemental Figure S2. Individual and interactive effects of fish size and temperature on time-integrated fish carcass decaying coefficients (k) for (**a**) dry mass (**b**) Carbon. Data points are mean (n=3) and error bars are ± 1SEM. Different letters above treatments indicate significant statistical differences among one another (Tukey's pos hoc test; $p<0.05$).



Supplemental Figure S3. Individual and interactive effects of fish size and temperature range on average Q_{10} values calculated as the ratio between time-integrated fish carcass decaying coefficients (k) for each temperature level. (**a**) dry mass and (**b**) carbon.

Population data

Here we present a 20 years times series representing the dynamics of phosphorus stored in carcasses over time separately for different age classes (Figure S4).

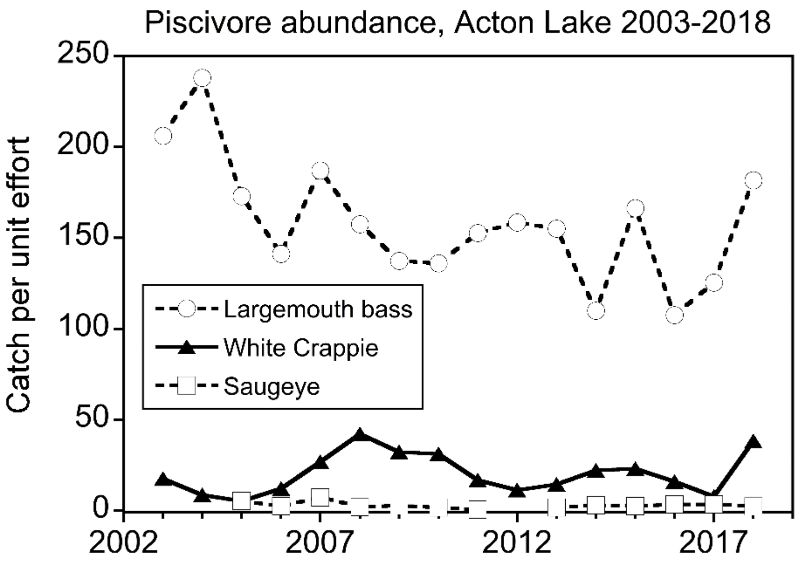


Supplemental Figure S4. 20-year time series showing the dynamics of phosphorus stored in gizzard shed carcasses accordingly to fish age class. Black line indicates age 0, orange line age 1, dark magenta line age 2, grey line age 3 and light purple age 4+. Nitrogen dynamics presented a very similar pattern (data not shown).

Piscivory Scenarios

The fluxes of N and P through piscivores in our model are based on the assumption that piscivore biomass is constant over the 20 years. Our model also assumes that piscivores account for 15% of the mortality of gizzard shad smaller than 200 mm total length, when temperature was >10°C; when temperature is <10°, piscivory is zero. Although both assumptions are based on data from Acton Lake, we explored additional scenarios in which we relaxed assumptions about piscivore abundance and piscivory rate.

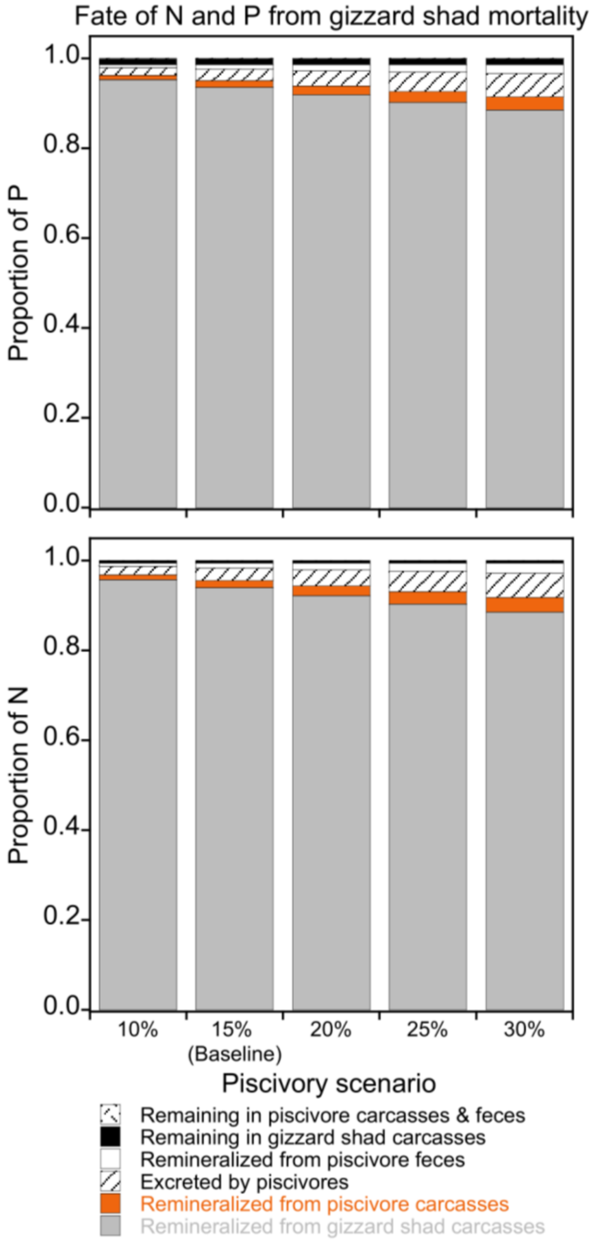
Piscivore abundance. The relative abundance of piscivores (catch per unit effort, CPE) in Acton has been assessed annually since 2003 by the Ohio Department of Natural Resources-Division of Wildlife. Those data suggest that largemouth bass are by far the most abundant piscivore (Figure S5), although the three piscivore species are captured with different methods and at different times of the year, so CPE data are not directly comparable among species. However, other analyses show that largemouth bass accounts for most of the piscivory in Acton Lake (Aman 2007). Largemouth bass CPE declined from 2003/2004 through 2008, but remained relatively stable after that, but with substantial interannual variation (Figure S5). Thus, from 2003-2015 (i.e., the last 13 years of our 20-year study), accumulation of nutrients in piscivore biomass was not likely to be a nutrient sink; on the contrary, the decline in bass CPE suggests that mortality exceeded births, and thus more nutrients were being ‘lost’ to the piscivore carcass pool than were being sequestered by living piscivore biomass. If so, we may have actually underestimated total mineralization from piscivore carcasses. Nevertheless, it is possible that piscivore CPE increased from 1996 (our first year) to 2003 (the earliest year for which piscivore data are available). We explored the potential consequences of this with a simple scenario, and compared it to the ‘baseline’ (constant piscivore biomass). We assumed that piscivore biomass doubled from 1998 to 2003 and that initial biomass was 20 kg wet mass/ha. Thus, piscivore biomass increased from 20 to 40 kg/ha over a 5-year period. Assuming that piscivore bodies are 10% N and 3% P by dry mass and a dry:wet mass ratio of 0.25, this equates to an increase of 500 g N and 150 g P/ha sequestered in living piscivore biomass over 5 years. Thus, we assumed that living piscivore biomass increased by 100 g N and 30 g P/ha/year, with an equal reduction in N and P ‘lost’ as piscivore carcasses relative to the baseline model. Over the 5-year period, this resulted in a decrease of available N supplied to the water column via the combined fluxes of piscivore carcass mineralization, piscivore excretion, and piscivore feces mineralization from 757 (baseline) to 657 g N/ha/yr, a 13% decline. For P fluxes via these processes, the doubling of live piscivore biomass resulted in a decline from 202 (baseline) to 172 g P/ha/yr, a 15% decline. However, all of the fluxes of available nutrients through piscivores (remineralization of piscivore carcasses and feces, plus piscivore excretion) together represent <6% of the flux via remineralization from gizzard shad carcasses. Therefore, the total effect of doubling piscivore biomass on N and P supply to the water column is very small (<1% compared to baseline). Furthermore, doubling of piscivore biomass over 5 years seems quite unlikely. Therefore, we conclude that our assumption of constant piscivore biomass over the 20-year period has little effect on our conclusion that nearly all of the N and P produced by gizzard shad mortality is returned to the water column in a form available to phytoplankton.



Supplemental Figure S5. Relative abundance (catch per unit effort) of piscivores in Acton Lake from 2003-2018. Saugeye are not native to Acton Lake and YOY were stocked annually beginning in 2004; no data are available for saugeye before 2005 or in 2012. Largemouth Bass were collected with electrofishing in spring, white crappies with trap nets in early autumn (September–October), and saugeye with gill nets in late fall (October–November). Data provided by J.D. Conroy, Ohio Division of Wildlife.

Piscivory rate

In our 'baseline' model we assumed that piscivores account for 15% of the mortality of gizzard shad smaller than 200 mm total length, when temperature was >10°C. In other words, for gizzard shad <200 mm and when temperature was >10°, 85% of gizzard shad dying in the lake were deposited on the lake bottom as carcasses, while 15% were consumed by piscivores. We ran additional simulations in which the percentage consumed by piscivores was increased to 20, 25 or 30%. In addition, we ran a simulation with the percentage set at 10%, i.e., less than baseline. In all cases, other aspects of the model were the same as in the baseline scenario. Changing the rate of piscivory had little effect on the ultimate fate of N and P, i.e., the total amount of N and P returned to the water column in available form changed very little (Figure S6). As % piscivory increased, the amounts of N and P mineralized directly from gizzard shad carcasses declined, although mineralization of shad carcasses was still by far the largest flux for both elements (Figure S6). Furthermore, the reduction in mineralization from shad carcasses was accompanied by compensatory increases in N and P remineralization from piscivore carcasses and feces, and piscivore excretion. Therefore, the total fluxes N and P to the water column, from all sources combined, were very similar among scenarios (Figure S6). In all scenarios, the amount of N remaining in carcasses (gizzard shad plus piscivores) was <0.6 % of the N produced by shad mortality; for P this percentage was <1.4% in all scenarios. Thus, the percentage of gizzard shad mortality caused by piscivory has little effect on the ultimate fate of N and P produced by gizzard shad mortality, because nutrients consumed by piscivores are eventually mineralized.



Supplemental Figure S6. Output from scenarios varying piscivory rate. In the baseline scenario, piscivores account for 15% of the mortality of gizzard shad smaller than 200 mm total length, and when temperature was >10°C. In the other scenarios, this percentage was varied from 10-30%. The y-axis refers to the proportion of N and P produced by gizzard shad mortality (flux via direct mortality plus shad eaten by piscivores). Note that the proportions of N and P remaining in piscivore carcasses and feces are included in the legend but are too small to visualize.

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