The impacts of global and local change on a tropical lake over forty years

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Running head: Forty years of change in a tropical lake

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Abstract

Lakes across the world are experiencing novel trophic states, declining water quality, and altered biogeochemical cycling due to the synergistic impacts of global change and local anthropogenic stressors. In the tropics these changes can be difficult to assess due to a lack of continuous monitoring or documented legacy conditions to serve as a reference for the contemporary lake. Over the last forty years, Lake Yojoa, located in west central Honduras, has shifted from an oligotrophic to mesotrophic ecosystem as evidenced by a loss of water clarity. To assess the changes that have occurred in Lake Yojoa as well as putative drivers for those changes, we compared secchi depth, dissolved inorganic nitrogen, and total phosphorus concentrations between 1979-1983 and today (2018-2020). While we found little change in total phosphorus between legacy and contemporary data, we found concurrent changes to seasonal trends in secchi depth and dissolved inorganic nitrogen (DIN). Seasonal peaks in DIN coincident with mixus suggest that accumulation of ammonium in the hypolimnion during stratification, and release to the epilimnion with mixus maintains algal productivity in what was previously a nutrient-limited, clear water phase, driving a change in the overall trophic state of Lake Yojoa. This impact of seasonal dynamics on the trophic state of the lake illustrates a key distinction in how physical structure and nutrients interact differently in tropical and temperate lake ecosystems and highlights the importance of warm anoxic hypolimnions to the biogeochemistry that governs the trophic state of tropical lake ecosystems.

Introduction

Global change affects lake ecosystems in a myriad of ways. The warming of surface water can alter stratification regimes and water column stability (Sahoo et al. 2016; Magee and Wu 2017) as well as intensify eutrophication (Moss et al. 2011). In some regions, increased nitrogen supply has shifted the macronutrient that limits primary productivity from nitrogen (N) to phosphorus (P) (Elser et al. 2009; Ackerman et al. 2019). Global change is also responsible for declining fisheries productivity (O'Reilly et al. 2003), changes in greenhouse gas emissions (Delsontro et al. 2018) and changes in dissolved N:P stoichiometry (Isles et al. 2017) in lake ecosystems. These impacts are often exacerbated by local anthropogenic stressors including over exploitation of resources, as well as enhanced loading of nutrients and organic pollutants from the surrounding watershed (Farrell et al. 2020).

Understanding how ongoing global change is impacting tropical lakes presents a major challenge in limnology because tropical lakes have historically been understudied compared to temperate lakes. As a result, the vast majority of our current understanding of freshwater nutrient cycling is derived from the study of temperate lakes (Kilham and Kilham 1990; Saulnier-Talbot et al. 2014). This is, in part, due to the abundance of lakes at temperate compared to tropical latitudes (Verpoorter et al. 2014). Further limiting our understanding of tropical lake nutrient dynamics is a relative lack of long-term monitoring efforts in tropical and subtropical lakes (Sarmento 2012). The largest body of work on tropical lakes are studies of the African Great Lakes (Talling and Lemoalle 1998; Guildford and Hecky 2000; Hecky 2000; Bootsma and Hecky 2003; Llirós et al. 2012;), with some notable exceptions such as work done in Lake Atitlan, Guatemala (Corman et al. 2015; Weisman et al. 2018) and in several Brazilian reservoirs (Pinto Coelho 1998; Tundisi et al. 2004). While studies of the African Great Lakes have made invaluable contributions to tropical limnology, the distinct lack of comparable research in other regions of the tropics and in lakes differing in size and stratification regime (Cael and Seekell 2016; Dodds and Whiles 2019) may bias our understanding of tropical limnology towards these unique ecosystems.

Despite the critical role temperate lake studies play in the understanding of aquatic ecosystem nutrient dynamics, we cannot directly translate knowledge derived from temperate lake studies to tropical lake studies because of inherent differences in climate and seasonality that occur across latitudinal gradients (Gardner et al. 1998). As temperature is unlikely to directly limit biogeochemical rate processes in tropical lake ecosystems (Talling and Lemoalle 1998), redox conditions and light availability are most likely to act as dominant controls over biogeochemical processes (Kilham and Kilham 1990).

While temperature often does not directly limit nutrient cycling in tropical lakes, temperature does have an important influence on the stratification regime (Lewis 1996). Temperate regions experience large seasonal variation in ambient temperature, resulting in predominantly dimictic lakes. Dimictic lakes mix in their hemispheric spring when ice-off occurs and surface temperatures begin to warm and again in autumn when air temperatures cool and minimize differences in the density between epilimnetic and hypolimnetic waters. In contrast, lakes in tropical and subtropical regions that are deep enough to maintain stable stratification are typically monomictic, mixing only once in their hemispheric winter (Talling 1969). The time between the onset of stratification and a single mixing event creates prolonged periods of anoxia in the hypolimnion. This anoxic period is potentially highly biogeochemically active due to the high temperature (>20°C) of the hypolimnion in tropical lakes (Lewis 1996). It is likely that tropical lake hypolimnions select for anaerobic pathways that may be thermodynamically constrained in the hypolimnions of temperate lakes. Thus, there is the potential for tropical hypolimnions to exhibit accelerated and possibly unique biogeochemical pathways which have a larger influence on ecosystem dynamics relative to temperate systems.

Anoxic biogeochemical processes in the hypolimnion in tropical lakes potentially include multiple anaerobic N transformation pathways. The rates of these pathways, such as dissimilatory nitrate reduction to ammonium (DNRA) and denitrification, have been found to exceed rates found in cooler, temperate systems (Lewis 1996; Li et al. 2019). N loss through denitrification, which occurs with little lag time once anoxic conditions establish, is often the proposed mechanism of N limitation in tropical lakes due accelerated denitrification (Kalff 1983; Zumft 1997). Additionally, anaerobic ammonium oxidation (anammox) has been documented in tropical systems, providing another possible N loss pathway (Schubert et al. 2006). While tropical lakes are not exclusively N limited (Melack et al. 1982; Kalff 1983; Elser et al. 2007), N limitation has been reported to be more common at lower latitudes than in temperate lakes (Prowse and Talling 1958; Talling 1969; Lewis 1974). However, discerning patterns of N limitation across the tropics may be complicated by shifting states of limitation driven by gradual climate changes (Ballantyne et al. 2011) and acute changes caused by extreme weather events (Corman et al. 2015). Understanding how interactive global and local effects alter biogeochemical pathways in tropical lakes will require coordinated and continuous research efforts aimed at evaluating the underlying mechanisms of ecosystem change.

To address ecosystem change in a tropical lake we compared two intensive sampling campaigns that occurred in Lake Yojoa (Honduras C.A.) forty years apart. The first campaign sampled Lake Yojoa at three locations fortnightly from 1979 to 1983 (henceforth referred to as legacy sampling, Vaux and Goldman 1984). To create a comparative contemporary dataset, we sampled the lake at five pelagic stations (including three sites aligned with the legacy locations) every 16 days from 2018 to 2020. We then analyzed our contemporary results in concert with those from the legacy sampling campaign. The objectives of this study were to 1) identify changes in Lake Yojoa's trophic state over the past forty years 2) identify differences in inter and intra-annual patterns in trophic state 3) evaluate the potential drivers of any observed changes in trophic state over the past forty years, and 4) understand how drivers of trophic state may differ between temperate and tropical lake ecosystems.

Methods

Study site

Lake Yojoa, located in west central Honduras (Figure 1), is the largest freshwater lake in the country and the economic backbone of the surrounding region. Apart from supporting local livelihoods (e.g. fishing, agriculture, recreation, tourism), Lake Yojoa and its watershed also foster exceptional biodiversity. The watershed provides habitat for over 400 species of birds, many of which are migratory, accounting for 44% of avian diversity found in North America

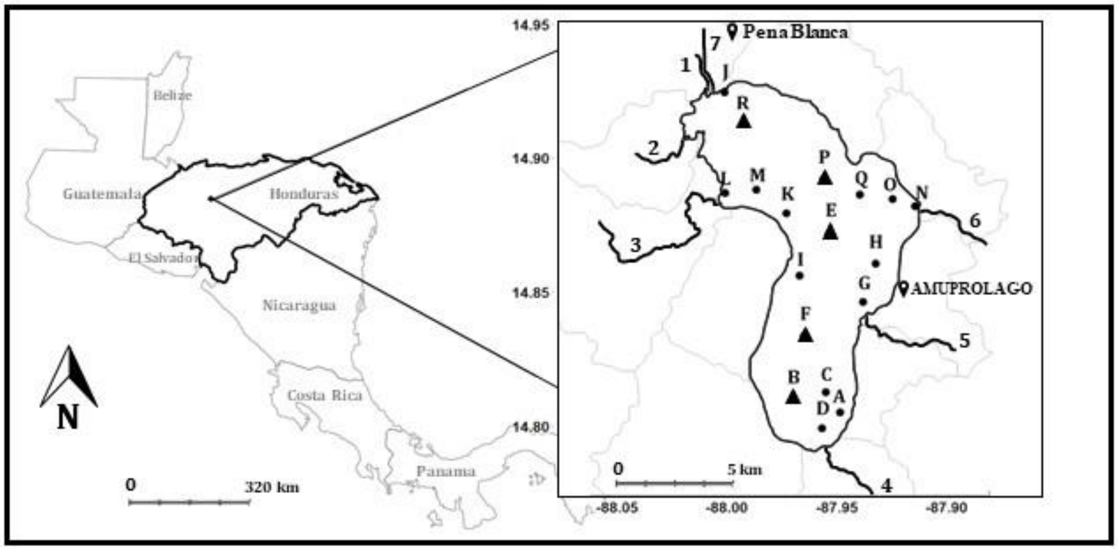
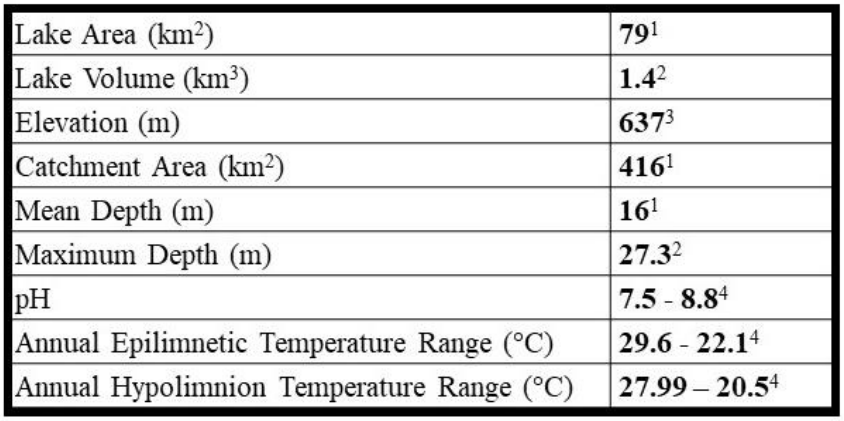


Figure 1. Stations within Lake Yojoa for biannual (A-R) and bimonthly (B, E, F, R and P) sampling. Tributaries and outflow: 1) Rio Helado 2) Rio Balas 3) Rio Raices 4) Rio Varsovia 5) Rio Cacao 6) Rio Yure 7) Canal (outflow)

Table 1. Physical characteristics of Lake Yojoa 1) Vaux 1993 2) Romero and Pineda 2007 3) Ramos et al. 1997 4) as measured by this study.



Lake Area (km^2)	**79^1**
Lake Volume (km^3)	**1.4^2**
Elevation (m)	**637^3**
Catchment Area (km^2)	**416^1**
Mean Depth (m)	**16^1**
Maximum Depth (m)	**27.3^2**
pH	**7.5 - 8.8^4**
Annual Epilimnetic Temperature Range (°C)	**29.6 - 22.1^4**
Annual Hypolimnion Temperature Range (°C)	**27.99 – 20.5^4**

(Gallardo et al. 2015). In addition, Parque Nacional Cerro Azul Meambar in the eastern watershed, and Parque Nacional Montaña de Santa Barbara in the western watershed provide important refuge for wildlife and contain many of the watershed’s 802 identified plant species (Studer 2007). Lake Yojoa also has a long history of being home to human populations. Archeological and paleolimnological records show continuous habitation of the watershed from 4500 years before present until as recent as 800 years before present (Rue 1987).

Today, the Lake Yojoa watershed houses nine municipalities with an estimated combined population of 74,624 (Rivera 2003) after seeing rapid population growth in recent decades (Boyd 2004). In 1974, 21,656 people lived in the Yojoa watershed (Dulin and Betancourt 1978). That number would increase by 68% over the next three decades, slightly outpacing the national population growth rate (House 2002).

Sample collection

All legacy data comes from the El Cajon Project (Vaux and Goldman 1984). From 1979 to 1983 samples were collected bimonthly at three pelagic stations. The most consistently sampled location (“Index”) aligns with contemporary station E while “Station 2” aligns with contemporary station F and “Station 1” is between stations R and P (Figure 1). Full details of sampling and analyses are available in Vaux and Goldman (1984). Briefly, duplicate epilimnetic samples were collected in 2.5 liter Van Dorn bottles. In the field, one of the duplicate samples was filtered through glass fiber filters, Grade GF/C and 0.45 µm HA Millipore filters using a Millipore Swinnex filter holder and syringe. The other sample was left unfiltered. Samples were analyzed for total phosphorus (TP), ammonium (NH_4^+), and nitrate (NO_3^-) as described below. In addition, during each sampling event, temperature and dissolved oxygen (DO) profiles of the water column and secchi depth were recorded (Vaux and Goldman 1984).

For the contemporary sampling campaign we collected water samples every 16 days between March 2018 and January 2020 as well as measured secchi depth with temperature and DO profiles from five stations within Lake Yojoa in collaboration a local non-profit charged with maintaining the integrity of the lake and its watershed (Asociación de Municipios del Lago de Yojoa y su Área de Influencia, AMUPROLAGO, Figure 1). Secchi depth measurements and temperature and DO profiles continued on the same 16-day schedule through March 2020 for two complete years of trophic state and physical profile measurements. In addition to routine sampling at five stations, in June of 2018 and 2019 and January of 2019 and 2020 we collected epilimnetic and corresponding hypolimnetic samples at an additional 13 stations (18 sites in total, Figure 1). For all sampling events, temperature and DO profiles were measured at two-meter intervals using a Hydrolab MS5 Multiparameter Sonde (OTT HydroMet, Loveland, CO). All epilimnetic samples were collected at a depth of 1 meter with an opaque PVC Van Dorn Water Sampler (Beta Bottles Part # 3-1930-H65) and temporarily stored in opaque HDPE Nalgene bottles (Thermo Scientific DS21850032) and placed in a cooler. Hypolimnetic samples were collected similarly at all locations deep enough to be stratified during June sampling events. Samples were collected at a depth of two meters above the sediment (depths between 17-23 m) to ensure sampling occurred below the thermocline but far enough above the sediment to avoid contamination from the sediment. On land, whole water samples were frozen for TP analysis while NH_4^+ and NO_3^- samples were first filtered through 25 mm glass microfiber filters, Grade GF/F (Whatman part no. WHA1825025) via Polysulfone Filter Funnels (Pall Life Sciences 4204) and then immediately frozen. All samples were stored in 15 ml centrifuge tubes (Corning 352097) before being transported to Fort Collins, CO while frozen. All dissolved chemistry analyses were performed at the EcoCore facility at Colorado State University, Fort Collins, CO, USA as described below.

Nutrient enrichment bioassays

In January and June of 2019, forty-eight clear glass bottles (120-mL) were filled with lake water from station E after passing the water through an 80 µm mesh to remove dominant grazers. In addition to the unamended control group, three treatment groups were prepared with twelve replicates each: +N (as NH_4SO_4), +P (as K_2PO_4) and +NP (at the same concentrations). Concentration of nutrient amendments were chosen to approximately double estimated *in situ* concentrations of N and P (based on epilimnetic nutrient concentrations from March and June of 2018). N and P amendments in treatment groups in January 2019 were 84.35 µg L^{-1} and 7.83µg L^{-1}, respectively. In June 2019, N and P amendments in treatment groups were 44.10 µgL^{-1} and 29.24 µgL^{-1}, respectively. We incubated each mesocosm in an outdoor water bath positioned near the lake as to expose bottles to ambient surface light conditions but buffer diel changes in ambient temperature. After three days, algae from each bottle were collected on GF/F filters. Filters were folded, wrapped in tinfoil, and immediately frozen for transport to Fort Collins, CO. Within three days of sampling, chlorophyll *a* was measured on a 10-AU fluorometer (Turner Designs Part No. 10-AU-074) via extraction in 90% acetone with acidification to 0.003 N HCl with 0.1 N HCl (EPA Method 445.0). Algal response for each treatment was recorded as percent increase from the mean algal concentration within the control group. We used pre-acidification values (chlorophyll *a* plus phaeophytin) for all control and treatment mesocosms to better represent changes in total biomass throughout the duration of the experiment.

Dissolved chemistry analyses

For the legacy study, NH_4^+ was measured using the indophenol method (Solórzano 1969), NO_3^- was measured using the hydrazine reduction method (Kamphake et al. 1967) and TP was measured using the ascorbic acid-molybdate method (APHA 1975). For the contemporary sampling campaign, TP was measured using a colorimetric ascorbic acid assay (EPA Method 365.3) modified to be analyzed on a UV-STAR Microplatte, 96 well via Infinite M200 TECAN at 880 nm absorbance detection. Both NH_4^+ and NO_3^- were measured using a Flow Solution FS 3700 Automated Chemistry Analyzer (O.I. Analytical, College Station, TX). NH_4^+ was determined by German Standard Methods (DIN 38406), also an indophenol method. NO_3^- was determined via automated colorimetry (EPA Method 353.2) which, like legacy measurements relied on determination via diazotizing with sulfanilamide and coupling with N-(1-naphthyl)-ethylenediamine dihydrochloride. NH_4^+ and NO_3^- values are presented separately as NH_4^+-N and NO_3^--N as well as a combined value of dissolved inorganic nitrogen (DIN). We found no evidence to suggest that the chemical analyses between contemporary and legacy sampling campaigns were systematically biased by the methods used, allowing for a direct comparison between the two sampling campaigns.

Calculations and Statistical Analyses

All data analyses were performed in R (version 4.0.2). Schmidt stability index (SSI), an estimate of the amount of energy required to mix a stratified water column, was calculated using the package rLakeAnalyzer (version 1.11.4.1) (Winslow et al. 2017) with temperature profile data provided by Regal Springs (an aquaculture company that has an operation on Lake Yojoa and collects daily temperature profiles). Trophic state index (TSI) was calculated using secchi depth according to Carlson (1977).

$$TSI(SD) = 10[6 - \frac{\ln(SD)}{\ln(2)}]$$

Statistically significant differences between annual TSI and monthly dissolved inorganic nitrogen (DIN), total phosphorus (TP), secchi depth and SSI were tested using one-way ANOVA. Treatment groups in the nutrient enrichment bioassay were compared using Tukey's HSD (honestly significant difference) test.

Supporting data

Cumulative monthly precipitation magnitude and timing, used as a proxy for watershed inputs, was provided by Empresa Nacional de Energía Eléctrica (ENEE) for 1970 to 2005 and measured in Peña Blanca, Cortes (El Jarel Station: U018; 14.9375°, 88.0047°) a small town on the northern end of Lake Yojoa (Figure 1). Contemporary precipitation data was collected for this study at the AMUPROLAGO office (Figure 1) via HOBO U30 USB Weather Station Data Logger (Part # U30-NRC). To assess potential changes in precipitation regime, available data for the most recent 20 years was compared to precipitation data from 1970-1990. The impact of ENSO years on precipitation was evaluated using Tukey’s HSD test.

Results

Trophic state

We assessed changes in Lake Yojoa’s trophic state over the past forty years by comparing annual mean secchi depths between the legacy and contemporary sampling campaigns. Mean annual secchi depth from the legacy period (mean =7.3 ± standard deviation 2.0 m) was significantly (*p*<0.001, df= 101) lower than present day conditions (3.2 ± 1.0 m, Figure 2a).

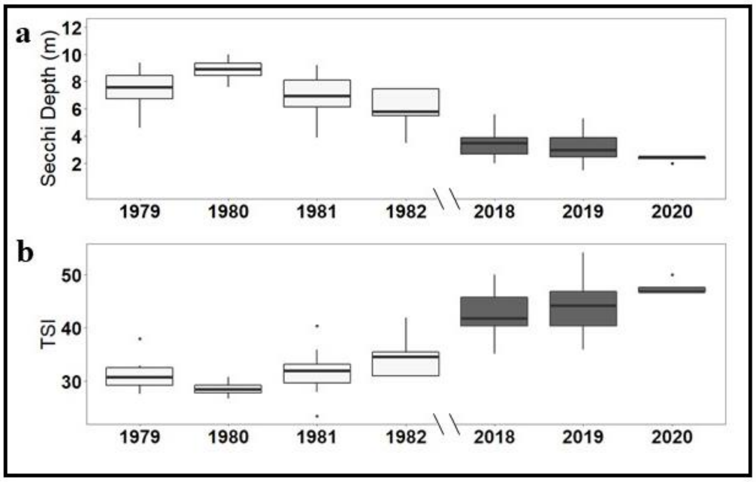


Figure 2. a) Secchi depth (meters) at station E across sampling years. **b)** Trophic State Index (TSI) for study years calculated with secchi depth (Carlson 1977).

Additionally, we calculated the lake's trophic state index (TSI) using secchi depth values and compared changes in mean annual TSI between the two sampling periods. TSI from the legacy period (31.12 ± 2.19) was significantly (*p*<0.001, df= 101) lower than present day conditions (44.28 ± 2.95, Figure 2b), suggesting that Lake Yojoa has shifted from oligotrophic to mesotrophic state over the past forty years.

We also assessed intra-annual changes in trophic state by comparing monthly mean secchi depth between the legacy and contemporary sampling campaigns. In the early 1980s, Lake Yojoa experienced an annual clear water phase from August to March (mean secchi =7.9 ± 1.7 m) with annual minimum secchi depth (5.0 ± 1.1 m) occurring between April and July (Figure 3a). Today Lake Yojoa shows no clear changes in water clarity among seasons. Secchi depth for the months that previously had the minimum secchi depth (April to July) now have, on average 37% lower secchi depths (mean secchi = 3.2 ± 1.0 m). The months that previously held a clear water phase (August – March) are now statistically indistinguishable (*p*=0.76, df= 75) from the remaining months (mean secchi = 3.2 ± 1.0 m).

Inorganic nitrogen and total phosphorus

To compare water chemistry between contemporary and legacy sampling, we assessed inter-annual and intra-annual changes in epilimnetic nutrient concentrations. For the legacy sampling

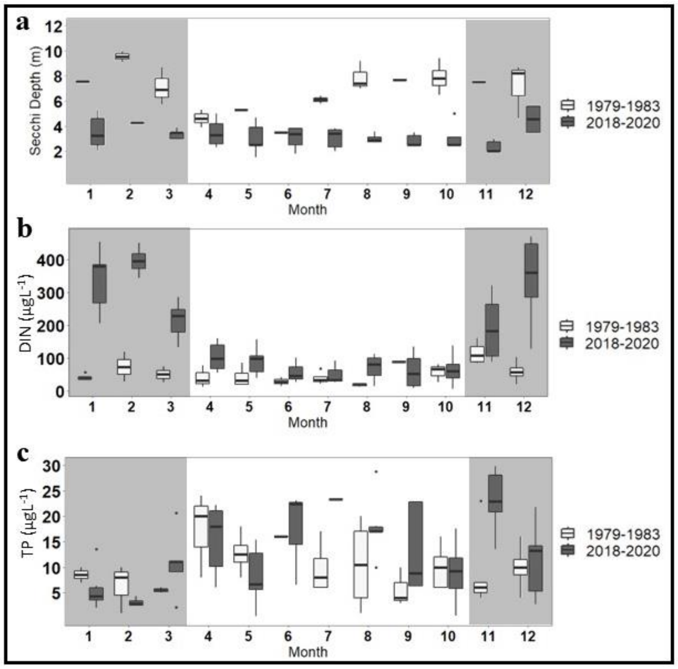


Figure 3. a) Secchi depth **b)** dissolved inorganic nitrogen (DIN) and **c)** total phosphorus (TP) at station E. Months with a mixed water column for the entire month or a portion of the month during 2018-2020 sampling shaded in grey.

period, dissolved inorganic nitrogen (DIN) varied throughout the year but exhibited no clear seasonality (54.97± 35.96 µg N L^{-1}, Figure 3b). During contemporary sampling, both mean annual DIN and intra-annual variation in DIN were greater than that observed during the legacy campaign (171.95± 138.03 µgL^{-1}, Figure 3b). Variation of DIN increased between legacy and contemporary sampling campaigns (65% vs. 80% annual variation, respectively). The increase in contemporary DIN was most pronounced directly following mixus in November (Figure 3b). After mixus, epilimnetic concentrations of DIN remained significantly higher (p<0.001, df=65) than pre-mixus levels until the onset of stratification in March when epilimnetic DIN concentrations returned to pre-mixus levels (Figure 3b).

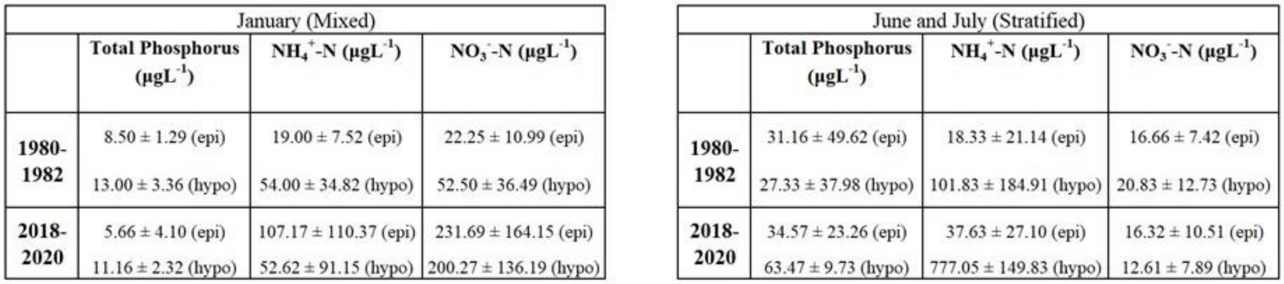
In contrast to DIN, contemporary TP values did not show increased seasonality in the contemporary period compared to the legacy period (Figure 3c). Mean annual TP values increased (approximately 75%) between legacy and contemporary campaigns (12.74± 19.47 µgL^{-1} and 22.34 ± 31.64 µgL^{-1}, respectively). This increase in TP is consistent with a shift in TSI from an oligotrophic to mesotrophic state (Salas and Martino 1991) and is thus accordant with observed changes in secchi depth.

TP concentrations for individual months were not significantly different between sampling campaigns except for November. In November, coincident with mixus, contemporary epilimnetic TP (68.25 ± 59.80) was significantly (*p*=0.047, df=15) higher than in the legacy sampling campaign (9.00 ± 7.90) (Figure 3c). However, unlike DIN, the observed peak in TP did not persist throughout the mixed period.

We compared differences in epilimnetic and hypolimnetic concentrations of TP, NH_4^+ and NO_3^- between legacy and contemporary sampling campaigns to test if the increase in epilimnetic DIN and TP following November mixus was driven by the release of accumulated hypolimnetic N and P. During the legacy sampling campaign, we observed no significant difference between epilimnetic or hypolimnetic concentrations of NO_3^- (*p*=0.504, df=9) or TP (*p*= 0.884, df=9) under stratified conditions (Table 2). While legacy hypolimnetic NH_4^+ concentrations appeared greater than epilimnetic NH_4^+ concentrations, the difference was not statistically significant (*p*= 0.298, df=9) (Table 2) and the accumulation of hypolimnetic NH_4^+ was not sufficient to enrich the epilimnion in NH_4^+ following mixus forty years ago (Figure 3b).

Today, during stratification, the hypolimnion of Lake Yojoa is significantly enriched in NH_4^+ (*p*<0.001, df=5) and marginally enriched in TP (*p*= 0.0781, df=7) relative to the epilimnion (Table 2). We observed no significant (*p*=0.67, df=5) difference in NO_3^- between the two strata

Table 2. Epilimnetic and hypolimnetic nutrient concentrations at station E (mean ± sd).



	January (Mixed)		
	Total Phosphorus (μgL^{-1})	**NH_4^+-N (μgL^{-1})**	**NO_3^--N (μgL^{-1})**
1980-1982	8.50 ± 1.29 (epi) 13.00 ± 3.36 (hypo)	19.00 ± 7.52 (epi) 54.00 ± 34.82 (hypo)	22.25 ± 10.99 (epi) 52.50 ± 36.49 (hypo)
2018-2020	5.66 ± 4.10 (epi) 11.16 ± 2.32 (hypo)	107.17 ± 110.37 (epi) 52.62 ± 91.15 (hypo)	231.69 ± 164.15 (epi) 200.27 ± 136.19 (hypo)

	June and July (Stratified)		
	Total Phosphorus (μgL^{-1})	**NH_4^+-N (μgL^{-1})**	**NO_3^--N (μgL^{-1})**
1980-1982	31.16 ± 49.62 (epi) 27.33 ± 37.98 (hypo)	18.33 ± 21.14 (epi) 101.83 ± 184.91 (hypo)	16.66 ± 7.42 (epi) 20.83 ± 12.73 (hypo)
2018-2020	34.57 ± 23.26 (epi) 63.47 ± 9.73 (hypo)	37.63 ± 27.10 (epi) 777.05 ± 149.83 (hypo)	16.32 ± 10.51 (epi) 12.61 ± 7.89 (hypo)

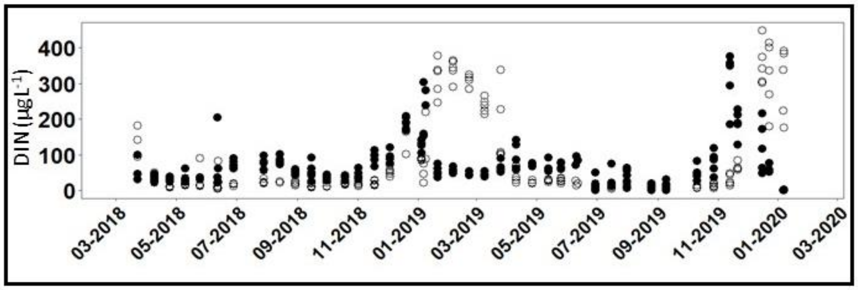


Figure 4. Epilimnetic ammonium (NH_4^+-N) (filled circles) and nitrate (NO_3^--N) (open circles) at stations B, E, F, P and R.

during the contemporary sampling period (Table 2). The prevalence of NH_4^+ relative to NO_3^- in the hypolimnion is consistent with the dramatic change in epilimnetic NH_4^+ that we observed in the contemporary lake directly following mixus (Figure 4).

Nutrient limitation

In order to assess the potential impacts of changing N dynamics on epilimnetic nutrient limitation, we calculated the molar ratio of DIN:TP in the epilimnion between the two sampling periods to use as a proxy for determining potential macronutrient limitation of primary productivity (Bergström 2010; Wetzel 2001). We used the ratio DIN:TP> 10 to suggest P limitation, 10>DIN:TP>5 to suggest co-limitation and DIN:TP <5 to suggest N limitation (Wetzel 2001). In the legacy period, we saw fluctuations in DIN:TP between 1.93 and 65.60; indicative of an ecosystem that alternated between states of N and P limitation (Figure 5a). In contemporary sampling we saw a greater annual range

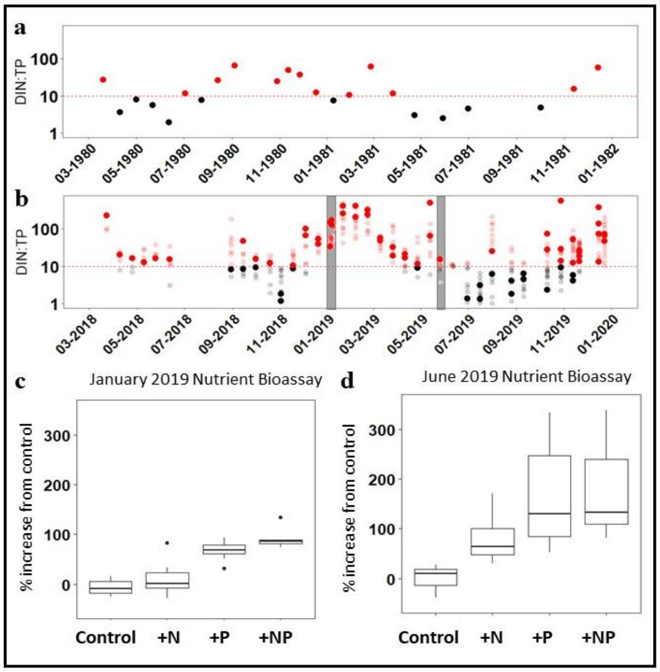


Figure 5. **a)** Legacy epilimnetic DIN:TP at location E **b)** contemporary DIN:TP at all locations (B, F, R, P and E bolded). Red indicates likelihood of P limitation above the red dashed line at DIN:TP = 10. P limitation threshold suggested by Wetzel (2001). Grey bars indicate timing of nutrient enrichment bioassays **c)** Nutrient enrichment bioassay from location E conducted January 2019. **d)** Nutrient enrichment bioassay from location E conducted June 2019.

of DIN:TP values (1.02 to 564.25) with a pronounced increase following November mixus (Figure 5b). This pronounced increase in DIN:TP values suggests that Lake Yojoa now experiences periods of pronounced P limitation that were not observed during the legacy sampling campaign.

To directly test macronutrient limitation in the contemporary epilimnion, we conducted two nutrient enrichment bioassays during 2019, one in January and one in June. In January, additions of N alone did not yield a significant increase in algal biomass relative to the control group (*p*=0.52, df=32). In contrast, algal biomass in the +P and +NP treatment groups was significantly greater than in both the control and +N treatments (*p*<0.001, df= 32, Figure 5c) though the +P and +NP groups were not significantly different from each other (*p*=0.18, df=32). Thus, P concentrations limited epilimnetic primary productivity in January. When we repeated the experiment in June, we found all treatments had a greater percent increase from the control than in January (Figure 5d). However, only treatments that received both N and P (+NP) were significantly different from the control group (*p*=0.054, df=17), suggesting N and P co-limitation during the June experiments. The results of the bioassays were consistent with limitations predicted from epilimnetic DIN:TP.

Potential Drivers

To assess the role of potential climatic drivers in the accumulation of hypolimnetic N and changing trophic state of Lake Yojoa, we compared legacy and contemporary water column stability using the Schmidt Stability Index (SSI). We hypothesized that if increasing air temperature led to an increase in water column stability between sampling periods, it would lead to a more pronounced and prolonged stratification period that would allow for an increase in NH_4^+ accumulation. Whereas cooler air temperatures and a less stable water column during the legacy period would have resulted in more frequent mixing and limited accumulation of NH_4^+during stratification. However, a comparison of monthly SSI suggested that contemporary thermal stratification may be weaker for seven (January, February, May, July, August, October and December) of the twelve months today compared to the legacy sampling period (Supplemental Table 1).

As reliable discharge measurements from Lake Yojoa's six tributaries were unavailable, we evaluated whether or not the precipitation regime of the Lake Yojoa watershed had changed between the two sampling campaigns, as watershed inputs of nutrients are likely to arrive primarily during the rainy season (Torres 1993; Pandey and Verma 2004). We hypothesized that changes in mean monthly precipitation between the legacy period and today may have led to increased loading of nutrients from the watershed or a shift in the timing of inputs between the two periods. Though we determined that the seasonal precipitation varied slightly between the two sampling campaigns, there was no significant difference in cumulative monthly rainfall for the Lake Yojoa watershed since 1970 ($p > 0.05$ for all months, df=29, Figure 6c). ENSO events appeared to have minimal effects on monthly cumulative precipitation, though the data suggests that October may be slightly drier in non-ENSO years (1982,

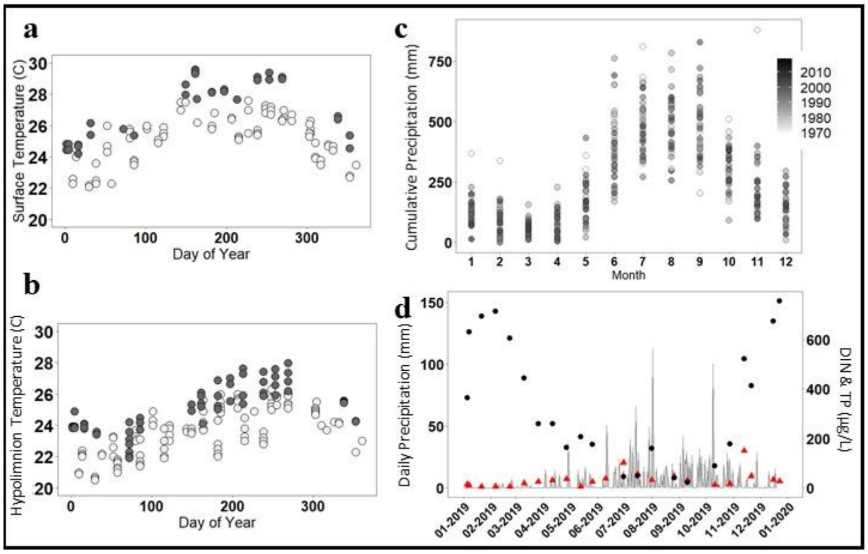


Figure 6. a) Surface and **b)** hypolimnion temperatures for legacy (light grey) and contemporary (dark grey) sampling. **c)** Cumulative monthly precipitation since 1970. **d)** Daily precipitation (primary axis) and mean epilimnetic DIN (black circle) at TP (red triangles) at locations B, E, F, P and R (secondary axis).

1983, 1987, 1988, 1991, 1997, 2005, *p*=0.027, df=22) compared to El Niño years. Despite these slight variations, there was no clear evidence that consistent changes in precipitation between the two sampling periods resulted in a shift in the magnitude or timing of watershed inputs to Lake Yojoa.

We also compared daily cumulative precipitation in 2019 to epilimnetic DIN and TP concentrations in the pelagic zone of the lake (B, E, F P, and R) to assess the relationship between peak rainfall events and pelagic nutrient concentrations. We found no corresponding increases in epilimnetic nutrient concentrations concomitant with large precipitation events for any of the five regularly sampled stations (Figure 6d).

Finally, we assessed the spatial distribution of contemporary hypolimnetic nutrient values during stratified conditions for June 2018 and 2019 sampling campaigns (Figure 7a-b). We hypothesized that if particulate nutrient load from tributaries was a major contributor to hypolimnetic nutrient accumulation, hypolimnetic dissolved nutrient concentrations would be greatest at sampling stations nearest tributaries (locations B, C, M, N, and O). However, mean hypolimnetic NH_4^+ concentration at stations nearest the tributary (546.77 ± 364.42) was approximately 17% lower than the total hypolimnetic mean (663.71 ± 255.30, Figure 7a). In contrast, hypolimnetic NH_4^+ at stations in the deepest portion of the lake, Q, P and R (781.56 ± 159.93) was, on average, approximately 17% greater than the total hypolimnetic mean. TP followed a similar trend with hypolimnetic TP concentrations nearest

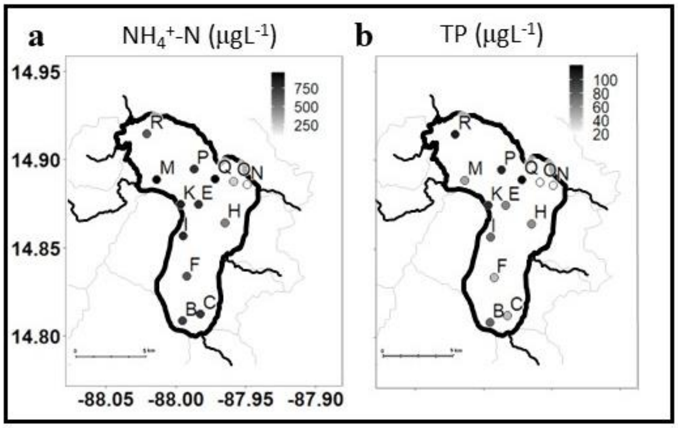


Figure 7. a) Ammonium (NH_4^+-N) and **b)** total phosphorus (TP) concentrations in the hypolimnion (June 2018 and 2019 means)

the tributaries (locations B, C, M, N, and O mean= 43.22 ± 23.05) being approximately 36% less than the total hypolimnetic mean (68.36 ± 23.05) and stations Q, P and R (101.84 ± 6.65) having 49% greater TP concentrations than the total hypolimnetic mean (Figure 7b).

Discussion

Comparison of legacy and contemporary sampling campaigns showed that over the past forty years Lake Yojoa has transitioned from an oligotrophic system with a distinct clear water phase (August to March) to a mesotrophic system with low water clarity and the absence of any pronounced seasonal differences in water clarity. This change in trophic state was accompanied by the development of novel, intra-annual N-cycling dynamics in which accumulation of hypolimnetic NH_4^+ during the stratified period resulted in a pulse of nutrients to the epilimnion during annual mixus (usually in November). Today, delivery of NH_4^+ to the photic zone during the dry season, when allochthonous inputs are at a minimum, maintains Lake Yojoa's mesotrophic state and prevents the development of the clear water phase that was present during the legacy period. To explore drivers and consequences of these altered biogeochemical dynamics in the context of the Yojoa watershed as well as a broader understanding of tropical limnology here we focus on 1) potential sources of nutrients to Lake Yojoa 2) putative biogeochemical pathways driving the N-cycling dynamics 3) differences in thermophysical lake structure between contemporary and legacy sampling, and 4) implications for changing nutrient dynamics in tropical lakes.

Sources of reactive nutrients to Lake Yojoa

Though this study did not explicitly aim to assess the sources of nutrients contributing to the changing trophic state of the lake, we can evaluate supporting evidence for several potential sources of nutrients to Lake Yojoa. Within the lake's watershed and the lake itself, a variety of economic activities support the resident population including: approximately 55 lakeside restaurants, a variety of agricultural activities (e.g., cultivation of yuca, sugar cane, coffee, and pineapple), subsistence fishing, industrial aquaculture, and ranching (Studer 2007). Recently, deforestation has further contributed to the anthropogenic footprint on the landscape and thus it is possible that changes in land use have altered the delivery of reactive nutrients to Lake Yojoa over the past forty years.

Increased hypolimnetic NH_4^+ concentrations near the mouths of each tributary would suggest that loading from the watershed may be driving the accumulation of hypolimnetic nutrients. However, hypolimnetic sampling stations in the littoral zone near the mouths of tributaries were not more enriched in NH_4^+ compared to sampling stations in the hypolimnion of pelagic zone of the lake (Figure 7a). Furthermore, if the majority of nutrients driving the lake’s productivity were derived from the watershed, we would expect to see an increase in epilimnetic nutrients during pronounced precipitation events. However, we found that rain events did not correlate with increases in epilimnetic DIN or TP (Figure 7d). If the majority of nutrients responsible for the eutrophication of Lake Yojoa were derived from the watershed, the observed asynchronicity between watershed loading and peak epilimnetic nutrient concentrations may be explained by rapid nutrient assimilation driven by co-limitation, as suggested by the June nutrient bioassays, leaving available nutrients in the dissolved phase for only a very short period. Alternatively, the disconnect between epilimnetic nutrient concentrations and rain events could also be explained by the subduction of cooler tributary waters and the formation of profile-bound density currents which could transport nutrients away from the littoral zone throughout the lake’s hypolimnion (Talling and Lemoalle 1998). However, the sampling stations nearest tributaries were depleted in nutrients relative to the stations in the hypolimnion of the pelagic zone of the lake. We propose that the lack of spatial or temporal correlation between the watershed inputs and water column nutrient concentrations are consistent with the watershed not being the main driver of nutrient changes in Lake Yojoa.

Within the lake itself there are two small “artisanal” net-pen Tilapia farms, one in the north-central region and one in the southern basin of the lake. In addition, there is a much larger “industrial” net-pen Tilapia operation in the north-central region of the lake (positioned nearest stations P, Q and R). Net-pen aquaculture, being unable to treat effluent and instead allowing waste materials to mix with the surrounding ecosystem, has been shown to increase the trophic state of its host lake and contribute to sediment nutrient concentrations (Troell and Berg 1997). Estimated nutrient loading from the industrial aquaculture operation in 2011 and 2013 ranged from 353 to 395 metric tonnes of N and 44 to 55 metric tonnes of P per year (*pers. comm*. Regal Springs). Carbon loading (both particulate and dissolved) from the Tilapia farm is also a significant consideration with possible loading estimates ranging from 81 to 91% (Gondwe et al. 2011) of C in feed ultimately transferring to the surrounding environment. However, exact C, N, and P loading may be difficult to compare across aquaculture operations given known differences in nutrient use efficiency of Tilapia caused by differences in stocking densities, mortality rates, and feed quality and quantity (Gondwe et al. 2011).

Another non-watershed potential source of N loading to Lake Yojoa is atmospheric N deposition. While N deposition values were unavailable specifically for the surface of Lake Yojoa, estimates for the region range from 67.56-87.13 mg N m^{-2} $year^{-1}$ (Dentener 2006). Given the surface area of Lake Yojoa (79 Km^2, Table 1), this would represent an annual deposition of between 5.3 and 6.8 metric tonnes per year which is approximately two orders of magnitude less than N loading from the aquaculture operation.

Biogeochemistry

It is also possible that the enhanced accumulation of NH_4^+ in the hypolimnion of Lake Yojoa may be due to selection of specific biogeochemical pathways that are more pronounced in tropical compared to temperature lakes. Here we consider four principal biogeochemical pathways that may result in the accumulation and retention of NH_4^+ in the hypolimnion of Lake Yojoa; nitrification, mineralization, dissimilatory nitrate reduction to ammonium (DNRA), and denitrification.

Shortly following November mixus and the pronounced increase in DIN in the epilimnion, we observed a rapid shift from NH_4^+ to NO_3^- as the dominant form of reactive N in the epilimnion (Figure 4). This was likely driven by nitrification. Due to the pronounced anoxia in the hypolimnion, nitrification is unlikely to play a role in the hypolimnetic N cycle. However, nitrification in the oxic portion of the water column is likely important to the initial supply of NO_3^- to other biogeochemical pathways that occur in hypolimnion after the onset of stratification.

We hypothesize that anaerobic process occurring in the hypolimnion may be key pathways that result in the accumulation of hypolimnetic NH_4^+ and the shifting trophic state of Lake Yojoa. Mineralization, which can occur through a variety of respiratory pathways both aerobic and anaerobic, is likely the dominant mechanism for generation of NH_4^+ in the hypolimnion. While organic N mineralization in the hypolimnion occurs at higher latitudes as well, the high temperatures present in the hypolimnion of Lake Yojoa lead to potentially accelerated rates of mineralization as seen in other tropical lakes (Gardner et al. 1998; Amado et al. 2013).

Warm conditions that contribute to increased mineralization rates in tropical lakes may also promote DNRA (Gruca-Rokosz et al. 2009), a second pathway leading to the accumulation of

NH_4^+. In other ecosystems, concentrated organic matter loading below aquaculture operations has been shown to increase DNRA rates seven-fold (Christensen et al. 2000). This introduction of organic matter is particularly important because under conditions of low NO_3^- and high labile C, DNRA is favored over complete denitrification, the dominant loss pathway for reactive N in most lake ecosystems (Nizzoli et al. 2010; Murphy et al. 2020). Given the large inputs of C that are likely associated with the industrial Tilapia operation in the deepest basin of the lake (nearest stations R, P and Q) these conditions are likely present in the pelagic hypolimnion of Lake Yojoa. Conditions that result in the selection for DNRA over denitrification would promote the accumulation of NH_4^+, whereas legacy conditions (e.g., lower organic C inputs) may have favored denitrification and prevented the accumulation of hypolimnetic NH_4^+.

To estimate changes in the rate of net hypolimnetic NH_4^+ accumulation we compared hypolimnetic concentrations of NH_4^+ between January when the water column was mixed and July near peak stratification between contemporary and legacy sampling periods. In the early 1980s, NH_4^+ accumulated in the hypolimnion at an estimated rate of 0.5 $\mu g\ L^{-1}\ day^{-1}$. Today, we estimate an accumulation rate of 4.7 $\mu g\ L^{-1}\ day^{-1}$ over the same period of time. This represents a nearly tenfold increase in the rate of NH_4^+ accumulation in the hypolimnion between the legacy and contemporary periods.

Thermophysical structure

Increasing water column temperatures in Lake Yojoa have decreased water column stability (Supplemental Table 1). The decrease in the stability of stratification is likely caused by warming of both the epilimnion and hypolimnion, lessening the density differences between layers (Figure 6a-b). As Lake Yojoa is presently a monomictic lake and was unlikely polymictic in the 1980s, as evidenced by greater SSI values in legacy data, the contemporary stratification conditions which allow for hypolimnetic nutrient accumulation likely existed in the 1980s though at a slightly reduced temperature.

The combination of decreased water column stability and hypolimnetic nutrient accumulation may make Lake Yojoa more susceptible to algal blooms associated with aseasonal mixing event. Mixing events during otherwise stratified months which introduce hypolimnetic nutrients to surface waters during peak annual temperatures may result in more frequent and more intensive algal bloom. One such bloom occurred on June 9th, 2020 and garnered national attention (La Tribuna 2020). These aseasonal mixing events may become more frequent with the continued warming of the region (Aguilar et al. 2005) and subsequent weaking of stratification stability combined with increased intensity of weather events predicted with climate change (Knutson et al. 2010).

Implications for tropical lakes

Algal biomass and thus trophic state in lakes is largely driven by nutrients, temperature, light availability and zooplankton predation (Bleiker and Schanz 1989; Zhang et al. 2018). However, the way in which these drivers define trophic state is different for temperate and tropical lakes. While many tropical lakes experience between-month variance in primary productivity which far exceeds any variances in incoming solar radiation (Vincent et al. 1986), primary productivity in temperate lakes is more strongly correlated to seasonal changes in solar radiation (i.e., light and temperature). Therefore, light and temperature limitations often seasonally constrain the phytoplankton community response to nutrient availability in temperate lakes. The impact of seasonal differences in solar radiation can be seen across monomictic (Peeters et al. 2007), dimictic (Arhonditsis et al. 2003) and polymictic (Adrian et al. 1999) temperate lakes, thus decoupling mixing regime from algal productivity. In contrast, in the absence of temperature limitations (*sensu* “the endless summer”) (Kilham and Kilham 1990; Hecky 2000), mixing events which deliver nutrients to the photic zone may have a profound impact on algal productivity in tropical lakes, making them fundamentally more sensitive to the timing of mixus and the associated hypolimnetic nutrient release.

The accumulation of NH_4^+ and subsequent release of nutrients into the non-temperature limited photic zone during the dry season when watershed inputs are minimal is a relatively recent development in Lake Yojoa. However, we hypothesize that a similar pattern of mixus and nutrient delivery during the dry season may be driving changes in trophic state in other tropical lakes as well. For example, the hypolimnion of Lake Maracaibo (Venezuela) is a site of organic matter accumulation and reduction processes, eventually releasing nutrients to the epilimnion (Parra-Pardi 1983). Similarly, winter mixus in Lake Titicaca (Peru-Bolivia) introduces large quantities of nutrients to the euphotic zone, temporarily alleviating previously observed N and P limitations (Vincent et al. 1984). These findings are consistent with the results from the nutrient bioassays in this study where we found Lake Yojoa to be co-limited by N and P under stratified conditions but primarily P limited following mixus.

The results from this study along with similar observations in other tropical lakes (Parra-Pardi 1983, Vincent et al. 1984) suggests that an increased understanding of hypolimnetic nutrient accumulation and release is necessary to better understand how global and local changes are affecting trophic state of tropical lake ecosystems. In monomictic tropical lakes, the interaction of the physical structure of the water column and nutrient loading places hypolimnetic processes at the intersection of local drivers (such as nutrient loading) and global drivers (such as climate change). Further research on tropical lakes should aim to understand the relationship between hypolimnetic nutrient accumulation rate, differences between epilimnetic and hypolimnetic nutrient concentrations, nutrient limitation, and seasonal changes to primary productivity to better predict how human activities are affecting tropical lakes globally.

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