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Water level fluctuations and the ecosystem functioning of lakes

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ABSTRACT

Hydrological regimes are key drivers of productivity and structure in freshwater ecosystems but are increasingly impacted by human activity. Using 17 published food web models of 13 African lakes as a case study, we explored relationships between seasonal and interannual water level fluctuations and 15 attributes related to ecosystem function. We interpreted our results in the context of Odum's ecosystem maturity hypothesis, as systems with higher magnitude fluctuations may be kept at an earlier maturity stage than those that are relatively stable. The data we compiled indicate that long-term changes in the hydrological regimes of African lakes have already taken place. We used Least Absolute Shrinkage and Selection Operator (LASSO) regression to examine relationships between ecosystem attributes and seven physical characteristics. Of these characteristics, interannual water level fluctuation magnitude was the most frequently retained predictor in the regression models. Our results indicate that interannual water level fluctuations are positively correlated with primary and overall production, but negatively correlated with fish diversity, transfer efficiency, and food chain length. These trends are opposite those expected with increasing ecosystem maturity. Interestingly, we found seasonal water level fluctuations to be positively correlated with biomass. An increase in standing biomass is generally associated with more mature ecosystems. However, we found that less production and biomass occurred at high trophic levels in highly fluctuating compared to relatively stable systems. This synthesis provides evidence that water level fluctuations are a key process influencing ecosystem structure and function in lakes.

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Introduction

Humans are altering hydrological cycles on local to global scales through the construction of impoundments, the extraction of water, and climate change (Poff et al., 2007; Döll et al., 2009; Haddeland et al., 2014). Water level fluctuations in freshwater ecosystems enhance productivity (Kolding and van Zwieten, 2012) and influence the timing and area of breeding habitat and other biological events among fauna (Lowe-McConnell, 1987; Gownaris et al., 2015). Seasonal pulses of water that carry nutrients from rivers or surrounding terrestrial ecosystems (Wantzen et al., 2008a) are especially important in relatively shallow, highly fluctuating lakes (Jul-Larsen et al., 2003). In deeper, stratified lakes, water level fluctuations influence internal nutrient

mixing (Zohary and Ostrovsky, 2011). Interactions within the aquatic/terrestrial transition zone, the portion of the littoral that fluctuates between wet and dry conditions with changes in water level, lead to the accumulation and resuspension of nutrient-rich organic matter and subsequently enhanced productivity (Junk et al., 1989; Lu et al., 2018).

Water level fluctuations also alter habitat availability, complexity, and quality. Depending on the morphology of the system, relatively minor changes in water level can lead to large variations in littoral habitat area (Kolding and van Zwieten, 2006; Gownaris et al., 2017). Newly inundated areas often have high habitat complexity (Wantzen et al., 2008a; Roy et al., 2018) and may be characterized by conditions unsuitable for large predatory fishes (Junk et al., 1989; Kolding, 1993a), thereby providing breeding and predator refuge habitat for some species (Mosepele et al., 2017). For example, Nile tilapia (*Oreochromis niloticus*) in Lake Turkana, Kenya find refuge from predators in shallow Ferguson's Gulf, where nocturnal oxygen conditions are too low for predatory Nile perch (*Lates niloticus*) and tigerfish (*Hydrocynus vittatus*) (Kolding, 1993a). Water level fluctuations may also influence habitat diversity by altering substrate availability (Gasith and Gafny, 1990) and the coverage and diversity of shoreline vegetation (Hill et al., 1998; Janssen et al., 2014).

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Though water level fluctuations can generate more productive and diverse habitats, they may also have undesirable effects on lake ecosystems and their services. Water level fluctuations may promote eutrophication and cyanobacterial blooms (Bakker and Hilt, 2016; Li et al., 2018) and increase susceptibility to invasive species (Zohary and Ostrovsky, 2011). As a form of environmental disturbance, an increase in water fluctuation magnitude may also affect lake biodiversity (e.g. in zooplankton, Lopes et al., 2014; in benthic invertebrates, Evtimova and Donohue, 2016; in fish, Jul-Larsen et al., 2003). Thus, both reducing and increasing the magnitude of water level fluctuations is likely to be associated with ecological and life-history trade-offs that have so far received limited attention for lake systems. Even in rivers, where the influence of water level fluctuations has been widely recognized for decades (e.g. Welcomme, 1979; Junk et al., 1989), research on the ecosystem-wide implications of changing hydrological regimes is largely nonexistent (Poff and Zimmerman, 2010). An improved understanding of how lakes will respond to climate and other hydrological changes is key to the adaptive management of these systems and their resources (Ogutu-Ohwayo et al., 2016; Paukert et al., 2017).

African lakes as a case study

We use African lakes as a case study on the ecosystem-wide impacts of water level fluctuations because they represent a diverse array of ecosystems for which comparable biological models have been developed. We use data from published Ecopath models, the most widely used modeling software in aquatic systems, to characterize these systems. Ecopath provides temporal ecosystem “snapshots” based on the principles of mass-balance (Christensen and Walters, 2004; Colléter et al., 2015). The current synthesis includes 17 published Ecopath models, representing 13 African lakes and one reservoir that cover a broad geographic range (Fig. 2, Electronic Supplementary Material (ESM) Table S1). These systems are also highly diverse in their physical and biological characteristics. Lake Nakuru (Kenya), for example, is a shallow, highly fluctuating system that hosts just one fish species. It has a maximum depth of <2 m and surface area of 45 km². Lake Tanganyika, in contrast, is a stable, stratified system with a maximum depth of >1400 m, a surface area of over 30,000 km², and hundreds of fish species. Patterns that hold across these systems are therefore likely to inform a broader array of freshwater systems globally.

Our focus on Africa is also driven by the importance and climate vulnerability of fisheries in this region (Ogutu-Ohwayo et al., 2016) and the dearth of studies on the impact of water level fluctuations on tropical and subtropical lakes (Leira and Cantonati, 2008). Recorded inland fisheries, which are likely to be significantly underestimated (Fluet-Chouinard et al., 2018), account for approximately one-third of Africa's capture fisheries production and employ over half of its fishers (FAO, 2014). Fish are a vital source of protein and nutrients, particularly in poverty-stricken regions of the continent (Youn et al., 2014; Kolding et al., 2016a). This continent is also likely to be one of the most vulnerable to climate change impacts, and many of its freshwater systems are already impacted by climate variability and change (i.e. temperature, wind speed, precipitation; Ogutu-Ohwayo et al., 2016; Barange et al., 2018).

Water level fluctuations can be regarded as an environmental disturbance that reduces the stability of an aquatic ecosystem (Jul-Larsen et al., 2003; Kolding and van Zwieten, 2012), therefore keeping it an earlier stage of maturity (Odum, 1969). Some lakes, such as Lake Nakuru, Kenya, or Lake Chilwa, Malawi, have high instability and may even intermittently dry up completely. The magnitude of water level fluctuations are therefore likely to influence attributes that change as an ecosystem develops (Odum, 1969). Specifically, we expect greater magnitude water level fluctuations to maintain or drive ecosystems towards an earlier stage of ecological succession. We compiled data on 15 ecosystem attributes related to ecosystem maturity (Table 1), either directly from Ecopath model publications or calculated using the data

available in these publications, similar to other published syntheses using Ecopath models (e.g. Pikitch et al., 2014).

Our work expands on previous syntheses of lake Ecopath models (Christensen and Pauly, 1993; Christensen, 1995) by examining models for 13 African lakes in the context of the magnitude of seasonal and interannual water level fluctuations of these systems. We aimed to answer the following questions: 1) What is the relationship between water level fluctuations at seasonal and interannual scales and the ecosystem attributes of lakes? and 2) Are the relationships between the compiled ecosystem attributes and increased water level fluctuations opposite to those expected with increased ecosystem stability and maturity? Our findings have implications for the productivity, resilience and composition of inland fisheries, which are likely to be of even greater global importance than currently recognized (Fluet-Chouinard et al., 2018).

Methods

Ecosystem models and biological attributes

The number of ecosystems studied was limited by the availability of published Ecopath models and water level data for African lakes. When two models, representing two distinct time periods, were available for a system, we used both (as in Christensen and Pauly, 1993; Christensen, 1995). These criteria led to a total of 17 models, representing 13 unique African lake systems (Fig. 2, ESM Table S1). In most cases, we obtained missing data directly from model authors, but data gaps persisted for some attributes.

A brief description of the Ecopath parameters used in this study and their related ecological attributes are included in Table 1; more detailed descriptions are given in Christensen et al. (2005). Prior to analysis, we converted all data for a given attribute to common units. To avoid confounding biomass-related attributes, we excluded the detritus pool from calculations, as has been done in previous analyses (Christensen and Pauly, 1993; Christensen, 1995). Attributes focused on: i) community energetics [i.e. total biomass (B), total production (P), primary production (PP), primary production over respiration (PP/R), primary production over biomass excluding detritus (PP/B), production over biomass excluding detritus (P/B), and biomass excluding detritus over total throughput (B/T)]; ii) community structure [i.e. the number of trophic levels through fish groups (NoTL), fish diversity (NoFish), and the system omnivory index (SOI)]; iii) nutrient cycling [trophic efficiency (TE)]; iv) overall homeostasis [respiration over biomass (R/B)], and v) catch related attributes [i.e. total catch (Catch) and mean trophic level of catch (MTL_C)] (ESM Table S2). These attributes were collectively used to address the two questions posed in the introduction. One model was missing a value for B/T (Lake Naivasha), and three models were missing the following attributes: TE (Lakes Awassa, Malawi, and Naivasha), MTL_C (Lake Nakuru models, Lake Tana), PP/R (Lake Naivasha and Lake Nakuru models), and R/B (Lake Navaisha and Lake Nakuru models). When missing values occurred, the Ecopath model was excluded from the regression model developed for that attribute.

Ecotrophic efficiency (EE) describes the proportion of production of a given functional group that is directly used in the system (e.g. eaten by predators or fished), and is often assumed to be 0.95 following Polovina (1984) or estimated by the Ecopath software. The average EE of the models used in this synthesis ranged from 0.31 to 0.95. We based our estimate of fish diversity on background information given in model publications and, when that was not available, on the species list for that system in FishBase (Froese and Pauly, 2015).

We calculated the maximum trophic level (TL_{max}) as fractional trophic level based on the published diet matrix for each model. Although birds are present in all African lake ecosystems, only four systems included bird trophic model groups (e.g. Lakes Hayq, George, Naivasha, and Nakuru). Because birds made up a very small portion of the total biomass where included (<1% in all models), we calculated TL_{max}

Table 1

Ecosystem attributes of study, the expected direction of their relationship (*sensu* Odum, 1969) with increasing maturity, and the direction of their relationship (this study) with increasing relative lake level fluctuations at interannual (RLLF_a) and seasonal (RLLF_s) scales. Trends listed as “NS” identify those for which the RLLF predictor was not retained in the regression model. Trends in bold are those in the opposite direction of what would be expected with increasing maturity. Where units are listed as “NA”, the attribute is unitless.

Ecosystem attribute (acronym)	Units	Definition/notes	Expected maturity trend (Odum)	Calculated trend	
				RLLF _a	RLLF _s
Community energetics					
Total biomass (B)	t/km ²	Sum biomass	Increase	NS	Increase
Total production (P)	t/km ² /yr	Sum production	Dome-shaped	Increase	NS
Primary production (PP)	t/km ² /yr	Sum primary production	Dome-shaped	Increase	NS
Primary production/respiration (PP/R)	1/yr	Sum primary production/sum respiration	Decrease	NS	NS
Primary production/biomass (PP/B)	1/yr	Sum primary production/sum biomass	Decrease	NS	Decrease
Production/biomass (P/B)	1/yr	Sum production/sum biomass	Decrease	NS	Decrease
Biomass/throughput (B/T)	1/yr	Sum biomass/sum of all flows	Increase	Increase	Increase
Community structure					
Number of trophic levels (TL _{max})	NA	Highest fractional trophic level	Increase	Decrease	NS
Number of fish (NoFish)	NA	Total number of fish species	Increase	Decrease	NS
Number of fish (NoFish)	NA	Total number of fish species	Increase	Decrease	NS
Nutrient cycling					
Trophic efficiency (TE)	%	Energy passed between trophic levels	Increase	Decrease	NS
Overall homeostasis					
Respiration/biomass (R/B)	NA	Schrödinger's ratio	Increase	Increase	Decrease
Other					
Catch (catch)	t/km ² /yr	Total catch	Decrease	NS	NS
Mean trophic level of catch (MTL _C)	NA	Average trophic level of catch	Increase	Decrease	NS

excluding these groups. To be certain that this choice did not influence our general findings, we ran our analyses including bird trophic model groups (TL_{maxb}) for comparison and found similar results whether or not these groups were included. The TL_{maxb} was slightly greater than TL_{max} in most systems (i.e. 1–9% increase in Lakes George, Hayq, Naivasha), but was 50% higher in Lake Nakuru, where the only fish trophic model group was tilapia that feeds on plankton.

To understand how decisions made by the model developers influenced our findings, we calculated a pedigree index (Christensen et al., 2005). The Ecopath pedigree routine is based on the quality of input data, was implemented in the early 2000s, and results in an index that ranges from 0 (poor quality model) to 1 (high quality model). Based on the data used to create the models, as described in the model publications and references therein, and on the tables in Christensen et al. (2005), we calculated index values for five key model components: biomass, productivity/biomass, consumption/biomass, diet composition, and catch. For example, for biomass the following scores were possible: 0.0 (guestimates, estimated from other model or by Ecopath), 0.4 (approximation or indirect method), 0.7 (low precision sampling), or 1.0 (high precision sampling) (Christensen et al., 2005). We calculated a total pedigree index for each model by averaging index values across trophic model groups and parameters. In a limited number of cases, the information needed to calculate an input parameter's index was not provided in the model publication (e.g. consumption/biomass for Lake Kariba, catch for Lakes Tana and Nakuru) and thus not included in the average.

Water level fluctuations and other physical predictors

Water level data availability varied by system and relied on gauge data for years preceding 1992 and satellite data for ensuing years (Table 2). We obtained gauge data from experts working on the system and, when this was not possible, extracted data from published figures using the software DataThief (Tummers, 2006). Satellite data were collected from the USDA/NASA Global Lakes and Reservoirs Database (G-REALM) or from Hydroweb (Crétau et al., 2011) and were available in approximately 10 day increments starting in 1992 for most systems (TOPEX/Poseidon satellite 1992–2003; Jason-1 satellite 2002–2009; OSTM satellite 2008–2015; USDA/NASA, 2015). These data are

published relative to the satellite's reference datum for each system and have an accuracy of approximately ± 10 cm (Crétau and Birkett, 2006).

Water level data were not obtainable for Lake George, Uganda. Instead, we used water level fluctuation data for Lake Edward, a system directly connected to Lake George via the Kazinga channel, to estimate Lake George water level fluctuations. Lake Hayq, Ethiopia was the only system for which no seasonal data could be obtained. The number of years with water level data available for each system ranged from 11 years (Lake Edward) to 112 years (Lakes Victoria and Turkana) (Table 2).

We conducted all statistical analyses using R Statistical Software (R Core Development Team, 2016). Because of the presence of outliers and heteroscedasticity in some of the water level fluctuation time series, we calculated temporal trends in water level fluctuations using the Theil-Sen estimator (Theil, 1950; Sen, 1968). Table 2 shows that significant temporal trends in interannual water level fluctuations existed for 7 out of 13 systems, approximately half of which were positive. Trends in seasonal water level fluctuations were significant for 10 of the systems and were positive for all but two (Table 2). Previous research has found that gauge and satellite data for African lakes are in strong agreement (e.g. L. Tana, $r^2 = 0.76$: Ayana, 2007; L. Victoria, $r^2 = 0.99$: Crétau et al., 2011; L. Kivu, $r^2 = 0.85$: Munyaneza et al., 2009), suggesting that water level fluctuation data obtained from these sources are comparable and complementary.

The degree to which water level fluctuations impact a given lake is highly dependent on the lake's average depth. As such, Kolding and van Zwieten (2006, 2012) proposed the use of relative lake level fluctuations (RLLF) in comparative studies. Relative lake level fluctuations are calculated as Average Amplitude / Depth * 100, where amplitude represents the difference between the maximum and minimum water level within a given year for seasonal fluctuations (RLLF_s) and the absolute difference between two sequential years for interannual fluctuations (RLLF_a) and where depth represents the mean system depth. We did not conduct any temporal smoothing prior to calculating amplitude.

Because water level data were not available for the periods represented by some ecosystem models (ESM Table S1), we chose to use the 1990s–2000s to calculate RLLF in all systems. We chose this time period because: 1) it was the most consistent period for which lake level data were available across systems, 2) it had some temporal overlap with the data used to develop several of the models in this study (7

Table 2
Average (1990s–2000s) and temporal trends in relative lake level fluctuations at interannual (RLLF_a) and seasonal (RLLF_s) scales. Trends at both scales were calculated using the Theil-Sen estimator, and significance levels are as follows: * ($p < 0.05$), ** ($p < 0.01$), *** ($p < 0.001$), NS (not significant). No seasonal data were available for Lake Hayq, so the trend for seasonal water level fluctuations is not applicable (NA). Gaps exist in some water level time series; the total number of years for which data were available in the listed range is shown in parentheses.

System	RLLF _a	RLLF _s	Range water level data (#years annual/seasonal)	1990s–2000s water level data (#years annual & seasonal)	Theil-Sen RLLF _a	Theil-Sen RLLF _s
Lake Tanganyika	0.04	0.13	1909–2014 ^a (106/106)	1990–2014 (25)	NS	↓**
Lake Kivu	0.13	0.46	1945–2008 ^b (35/35)	2003–2008 (13)	NS	NS
Lake Malawi	0.14	0.59	1921–2014 ^c (93/93)	1990–2014 (25)	↑*	↑***
Lake Victoria	0.64	1.31	1900–2014 ^d (112/112)	1993–2014 (22)	NS	↑***
Lake George	1.18	2.81	2000–2010 ^e (11/11)	2000–2010 (11)	NS	↓**
Lake Turkana	1.59	3.72	1888–2014 ^f (112/22)	1993–2014 (22)	↑*	↑***
Lake Tana	2.15	18.62	1960–2014 ^g (55/55)	1990–2014 (25)	↓**	↑**
Lake Chad	2.59	30.28	1954–2014 ^h (46/46)	1993–2014 (22)	↑*	↑***
Lake Kariba	3.97	15.02	1963–2014 ⁱ (52/52)	1990–2014 (25)	↓***	↑***
Lake Awassa	4.22	16.04	1970–1999 ^j (30/30)	1990–1999 (10)	↑***	↑***
Lake Hayq	8.85	NA	1975–2012 ^k (29/0)	1990–2012 (16)	↓*	NA
Lake Naivasha	11.32	28.34	1900–2014 ^l (110/110)	1990–2014 (20)	NS	↑***
Lake Nakuru	38.7	40.77	1958–2000 ^m (29/29)	1993–2000 (9)	NS	NS

^a 1909–1992: van Zwieten, pers. comm., data used in Kolding and van Zwieten (2012); 1993–2014: USDA/NASA (2015).

^b 1945–1973: van Zwieten, pers. comm., data used in Kolding and van Zwieten (2012); 2003–2008: Crétaux et al. (2011).

^c 1921–1992: van Zwieten, pers. comm., data used in Kolding and van Zwieten (2012); 1993–2014: USDA/NASA (2015).

^d 1900–1988: van Zwieten, pers. comm., data used in Kolding and van Zwieten (2012); 1993–2014: USDA/NASA (2015).

^e 2000–2010: Crétaux et al. (2011).

^f 1888–1989: van Zwieten, pers. comm., data used in Kolding and van Zwieten (2012); 1993–2014: USDA/NASA (2015).

^g 1960–1992: Kebede pers. comm., data used in Kebede et al. (2006); 1993–2014: USDA/NASA (2015).

^h 1954–1977: Coe and Foley (2001); 1993–2014: USDA/NASA (2015).

ⁱ 1963–1992: van Zwieten, pers. comm., data used in Kolding and van Zwieten (2012); 1993–2014: USDA/NASA (2015).

^j 1970–1999: Ayenew and Gebreegziabher (2006).

^k 1975–2012: Wonde and Dawud (2014).

^l 1900–1992: van Zwieten, pers. comm., data used in Kolding and van Zwieten (2012); 1993–2014: USDA/NASA (2015).

^m 1958–2000: Jenkins pers. comm., data used in Jenkins et al. (2009).

out of 17 models and 7 out of 13 systems), and 3) satellite monitoring for the systems of study began in 1992, so these data had high temporal resolution. We contend that our choice of time period did not influence our conclusions, as there was a strong positive correlation between the RLLF values calculated for the 1990s–2000s and the RLLF values calculated for the complete time series among systems at both interannual ($r^2 = 0.96$, $p < 0.0001$) and seasonal ($r^2 = 0.94$, $p < 0.0001$) scales. Lake level fluctuations were also highly correlated at seasonal and inter-annual scales across systems ($r^2 = 0.90$, $p < 0.001$).

The strength in RLLF as a physical predictor in freshwater ecology is in its combination of the important static physical measure of depth (Ryder et al., 1974) with that of the dynamic physical measure of water level fluctuations (Kolding and van Zwieten, 2012). There are a variety of static metrics that have been traditionally used to relate physico-chemical characteristics with productivity and species diversity in lakes. To explore the importance of physical characteristics other than RLLF in determining food web structure, data on these characteristics were collected from relevant online databases and publications. Where possible, data collection focused on the International Lake Environment Committee Foundation (ILEC) World Lakes Database for consistency across systems. Physical characteristics collected included i) climatic [latitude (Lat), altitude (Alt)], ii) morphologic [surface area (SA), volume (V), residence time (RT)], and iii) hydrologic variables [RLLF_s, RLLF_a, catchment area (CA)] following Kolding and van Zwieten (2012) (ESM Table S3). We also tested for relationships between model complexity and water level fluctuations to determine whether differences in model development could have influenced our results (e.g. Morissette, 2007; Heymans et al., 2014). We relied on the number of model groups (log-transformed) and the number of trophic links (normally distributed) of each model as indicators of model complexity.

Statistical approach

Our statistical approach was chosen to be appropriate for small sample sizes and the non-normal distributions of many of the physical

predictors and ecological attributes of interest. In recognition that col-linearity among RLLF and other physical predictors could drive or obscure relationships among RLLF and ecological attributes, we regressed each ecosystem attribute on a matrix of the physical characteristics described above. We first tested all variables of interest for normality using the Shapiro-Wilk test; most showed non-normal distributions and were natural log-transformed prior to analysis (ESM Table S4). All variables were normal after transformation.

Due to our low sample size, we tested only for linear relationships between ecological attributes and the physical predictors of interest. By excluding non-linear relationships, we are likely to underestimate the strength of some relationships (e.g. PP and TotalP may have a domed-shape relationship with RLLF; Table 1).

We performed all regressions using the Least Absolute Shrinkage and Selection Operator (LASSO) available in the glmnet package in R (Friedman et al., 2010). We used LASSO regression to test whether each ecological attribute was significantly correlated with the magnitude of water level fluctuations at seasonal and/or interannual scales when also considering the other physical characteristics we compiled. LASSO is a more robust regression approach than ordinary least squares (OLS) and stepwise model selection in the presence of small sample sizes and potentially colinear predictors (Tibshirani, 1996). The algorithms used to conduct LASSO regression in glmnet optimize the objective function over each parameter (i.e. one physical characteristic), holding all other parameters (i.e. the remaining physical characteristics) constant. This process is repeated until the model converges. We selected the regression model associated with the lambda value that resulted in the lowest mean cross-validated error.

The best-supported model resulting from the LASSO regression provided two key pieces of information: 1) Are water level fluctuations at seasonal and/or interannual scales predictors of ecosystem attributes after accounting for other, potentially co-linear, physical characteristics? and 2) If there is a significant relationship between the ecosystem attribute and seasonal and/or interannual water level fluctuations, what is the direction of the relationship? We compared the direction of

significant relationships with those expected with increasing ecosystem maturity (Odum, 1969), assuming that systems with higher magnitude water level fluctuations would be less stable and mature (Table 1). For example, an ecosystem's total standing biomass is expected to increase as that ecosystem matures, so total biomass might be expected to have a negative relationship with the magnitude of water level fluctuations. Because missing values are not supported in LASSO regression, we excluded Lake Hayq, for which there was no seasonal water level fluctuation data, from these regressions. Where data were missing for a specific parameter (e.g. biomass/throughput for Lake Naivasha), we excluded the relevant system(s) from the LASSO regression for that parameter, so final sample sizes ranged from 13 to 16 systems per regression model (ESM Table S4).

Because of their growing attention in the literature (e.g. Link et al., 2015; Kolding et al., 2016a), additional analyses were conducted to examine the influence of disturbance on the distribution of biomass and production in lakes. Lakes were categorized into two groups, high and low RLLF (Jul-Larsen et al., 2003); all 17 models compiled were used in this analysis. We defined the cut-offs for “high” and “low” RLLF based on the median of the values across systems. We defined all systems having an $RLLF_a \geq 2.15$ and $RLLF_s \geq 9.4$ as “high RLLF”. All lakes that fell below these values were considered “low” RLLF lakes. We compared these attributes between the high and low RLLF groups in two ways. First, we calculated the slopes of changes in log biomass and log production, respectively, with trophic level following Kolding et al. (2015, 2016a). Second, we examined relationships among cumulative average production, cumulative average biomass, and trophic level following Link et al. (2015).

Results

Ecosystem models and attributes

The majority of the Ecopath models examined in this study focused on ecosystem data collected in the 1970s–1980s (12 out of 17 models), with the remaining five models focusing on the 1990s–2000s (ESM Table S1). Fifteen ecological attributes related to fisheries or proposed

by Odum (1969) could be calculated using the available Ecopath data (Table 1, Fig. 1). The number of trophic model groups in each system ranged from 7 (i.e. pelagic zone of Lake Tanganyika) to 25 (Lake Malawi), with an average of 13 (ESM Table S1). The number of trophic links ranged from 18 (Lake Turkana) to 208 (Lake Malawi); the average number of links across models was 58 (ESM Table S1). The number of model groups or trophic links was not significantly correlated with $RLLF_a$ or $RLLF_s$ ($r^2 < 0.01$, $p \geq 0.70$ in all tests).

The pedigree index values calculated for all 17 models ranged from 0.41 (Lake Chad) to 0.72 (Lake Nakuru 1972), with an average of 0.56 ± 0.10 SD (ESM Table S1). Except for Lake Awassa, all models with a pedigree index value of <0.52 (Lakes Chad, Victoria, Naivasha, George, Tanganyika) relied on Ecopath-estimated biomass for most or all their trophic model groups. Our pedigree index was comparable to those published for the Lake Hayq (this study: 0.63; published: 0.64) and Lake Malawi (this study: 0.58; published: 0.61) models, and considerably lower than the published value for the Lake Tana model (this study: 0.57; published: 0.84). The difference between our estimated pedigree indices and those published may result from differences in judgement regarding data quality or from additional information known by the model creators but not evident in the model publication. In all cases, our pedigree indices were lower than those estimated by the model creators, suggesting that our evaluation of model quality was conservative. The pedigree index was normally distributed across models and was not significantly correlated with either $RLLF_a$ ($r^2 = 0.16$, $p = 0.11$) or $RLLF_s$ ($r^2 = 0.05$, $p = 0.39$).

Water level fluctuations and other physical predictors

$RLLF_a$ values varied from 0.04 (Lake Tanganyika) to 38.70 (Lake Nakuru), with 10 of the 13 systems having $RLLF_a$ values between 0 and 5 (Table 2). Put more intuitively, Lake Tanganyika fluctuates on average 0.04% of its mean depth from one year to the next, while Lake Nakuru fluctuates on average 38.70% of its mean depth. $RLLF_s$ ranged from 0.11 (Lake Kivu) to 40.77 (Lake Nakuru), but 9 of the 12 systems had $RLLF_s$ between 0 and 20 (Table 2). Data for the remaining physical

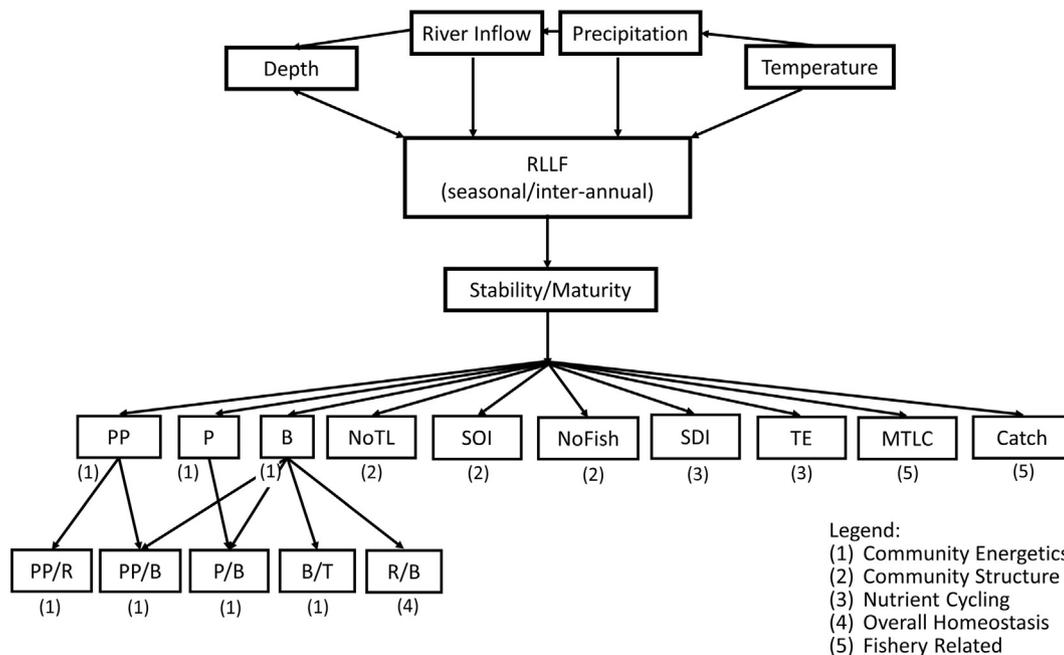


Fig. 1. Conceptual diagram showing connections between and among relative lake level fluctuations (RLLF), stability/maturity as defined by Odum (1969), and the ecological attributes of lakes (see Table 1 for acronym descriptions).

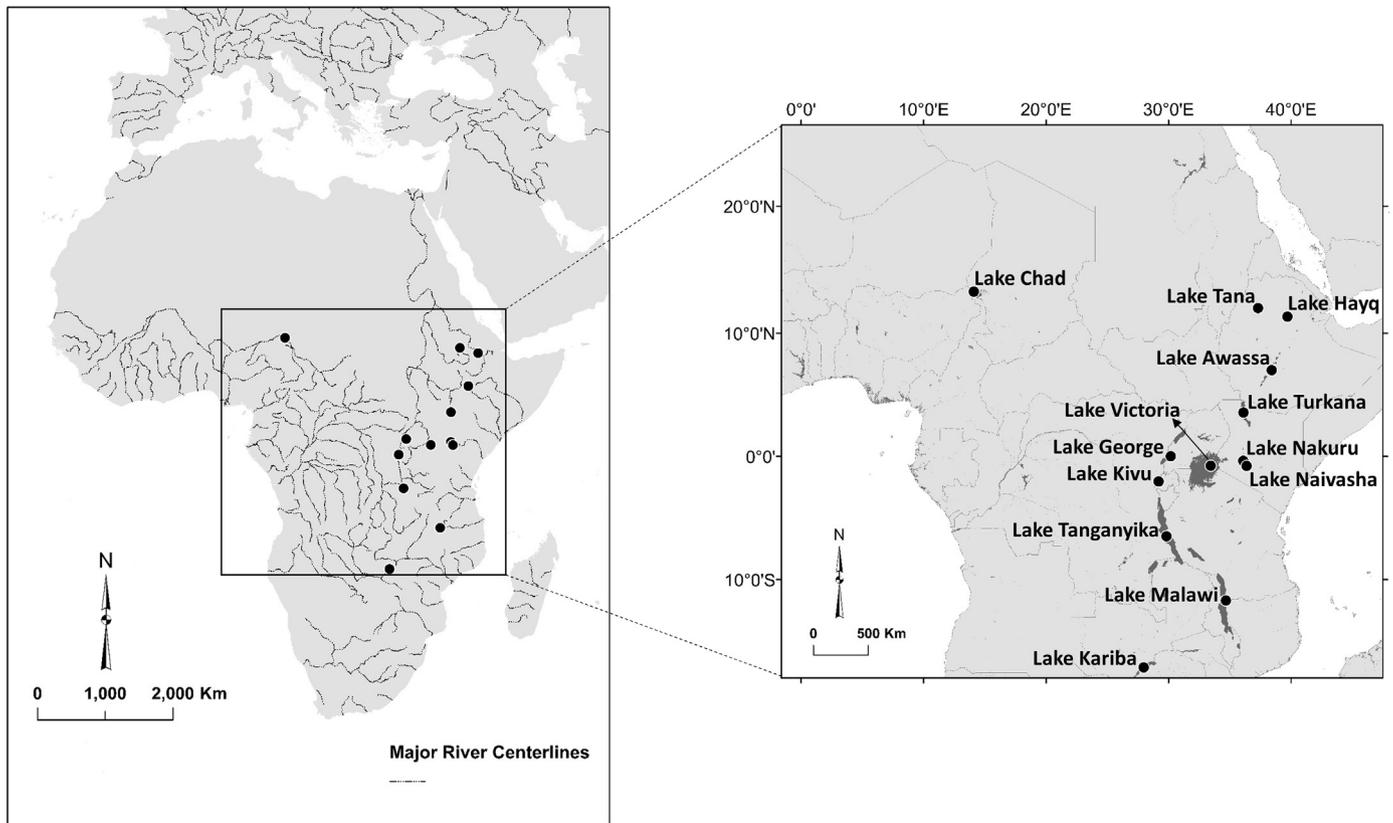


Fig. 2. Major river centerlines in Africa (Natural Earth, 2015) and locations of the 12 lakes and one reservoir (Lake Kariba) used in this synthesis. Base map was provided by Esri (2015).

characteristics included in the LASSO regression models are found in ESM Table S3.

Relationship between water level fluctuations and ecosystem attributes

Sample sizes for LASSO regression models ranged from 13 to 16 due to missing RLLF_s data for Lake Hayq and missing ecosystem attribute data for some Ecopath models (ESM Table S4). RLLF_a was retained as a significant predictor in nine out of 15 regression models. In six

regression models the relationship with RLLF_a was in the expected direction, i.e. opposite to that expected with increasing maturity (Table 1, ESM Table S4). RLLF_s was retained as a predictor in six out of 15 regression models; the relationship was opposite to that expected with increasing maturity in only one case (Table 1, ESM Table S4). All other physical predictors were retained in fewer models. The next best overall predictor was volume (V), which was retained in seven out of 15 regression models (ESM Table S4). Physical characteristics were not a significant predictor for the ecosystem attributes Catch and

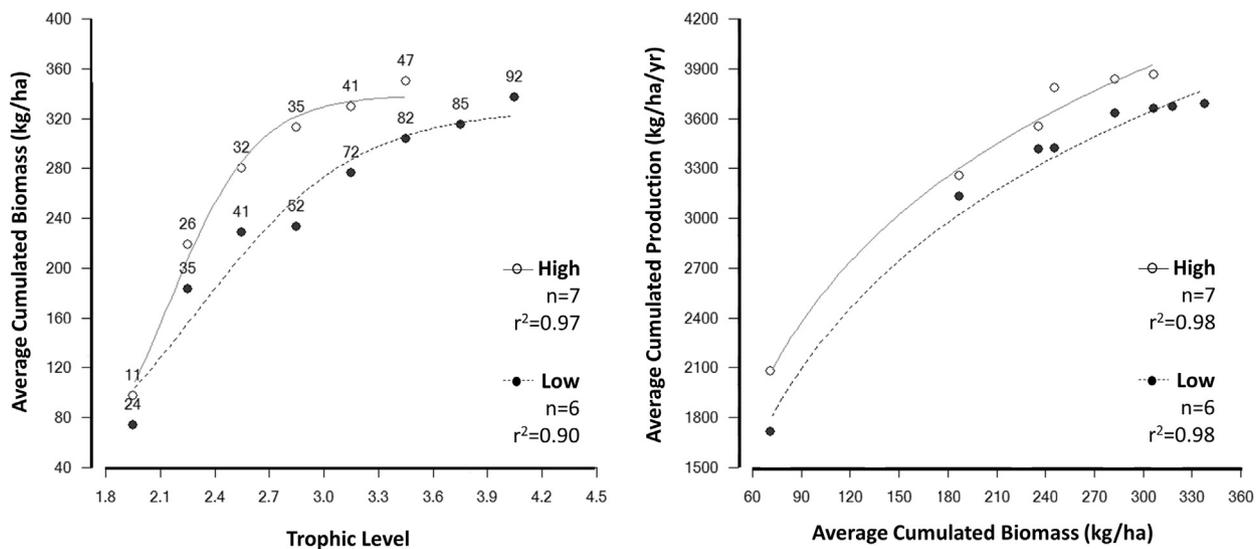


Fig. 3. Logistic regressions showing the relationship between (left panel) average cumulative biomass and trophic level (in bins of 0.3 trophic levels) and (right panel) average cumulative production and average cumulative biomass. The “High RLLF” category represents systems with interannual relative lake level fluctuations of ≥ 2.15 and intra-annual relative lake level fluctuations of ≥ 9.4 . Point labels in panels refer to the number of trophic model groups used to calculate average values and the correlation of the fitted lines.

primary production to respiration (PP/R) (ESM Table S4). Fish diversity (NoFish) and Schrodinger's Ratio (R/B) were the ecological attributes best described by physical characteristics, with r^2 values of >0.90 (ESM Table S4).

Increasing water fluctuations had a significant effect on trophic community structure (i.e. the Eltonian pyramid: Lindeman, 1942). Linear regressions of log-transformed biomass and production against mean trophic levels (TL) showed that biomass (high RLLF: $b = -0.59$, $r^2 = 0.92$, $p < 0.01$; low RLLF: $b = -0.31$, $r^2 = 0.73$, $p < 0.05$) and production (high RLLF: $b = -1.4$, $r^2 = 0.98$, $p < 0.001$; low RLLF: $b = -1.0$, $r^2 = 0.95$, $p < 0.01$) decreased at a faster rate as trophic level (TL) increased in high compared to low RLLF systems. Regressions between cumulative biomass and cumulative production and between cumulative biomass and TL were best described by logistic curves (Fig. 3), which are situated closer to the origin for low RLLF systems than for high RLLF systems. Inflection points for cumulative biomass occurred at a similar percent of cumulative biomass for both high and low RLLF groups, but the TL inflection point was lower for high RLLF systems than for low RLLF systems (Fig. 3).

Discussion

Water level fluctuations in lakes are a natural phenomenon associated with climate variability (Olaka et al., 2010). For example, the water level of Lake Nakuru was 45 times greater during the earlier Holocene than it is today (Olaka et al., 2010). However, hydrological regimes are being increasingly influenced by climate change, dam construction, and irrigation demands (Wantzen et al., 2008b). For African lakes, we found evidence that hydrological regimes are already changing, as nearly all systems analyzed in this study showed significant temporal trends in interannual and/or seasonal fluctuations.

According to model projections from the Intergovernmental Panel on Climate Change (IPCC), precipitation in East and Central Africa is expected to increase (Stocker et al., 2013). Observations to date do not seem to support this trend (e.g. Lott et al., 2013), but the prediction of increased variability in precipitation across the continent appears undisputed (e.g. Sahel: Dai et al., 2004; southern Africa: Tadross et al., 2005). Temperature changes will further influence hydrological regimes by altering the rate of evaporative water loss and mixing patterns (Bootsma and Hecky, 1993; Verburg et al., 2003; Ogotu-Ohwayo et al., 2016). In addition, the African continent is likely to experience considerable growth in dam construction over the coming decades (Zarfl et al., 2015), and therefore increasingly regulated hydrological regimes.

We found that nearly all of the lakes studied showed positive temporal trends in water level fluctuation magnitude (i.e. increasing magnitude over time), consistent with the drier dry seasons and wetter wet seasons expected by IPCC (Stocker et al., 2013; Niang et al., 2014). Hydropower development and subsequent flow regulation will likely have the opposite impact on water level fluctuation magnitude. In their review of climate change impacts on the water sector in Africa, Boko et al. (2007) noted increased instability of the water level of several African lakes since the 1960s (Lakes Victoria, Tanganyika, and Turkana) due to the occurrence of extreme drought and flood events. For example, using satellite altimetry data, Mercier et al. (2002) found widespread decreases in water level in nine African lakes (including Lakes Kariba, Malawi, Tana, Tanganyika, Turkana, and Victoria) from 1993 to 1997, which they attributed to extreme droughts, and rapid increases in water level in most of these systems from 1997 to 1998. The sudden increase in water level in 1997–1998 resulted from anomalously high rainfall in late 1997, which was associated with warming over the Indian Ocean during that year's ENSO event (Mercier et al., 2002).

Our analysis suggests that water level fluctuations, expressed relative to mean depth, may significantly influence the ecological attributes of African lakes. Water level fluctuations were retained as a predictor in a greater number of multivariate regression models than any other

physical characteristic. We found that, while seasonal and interannual fluctuations are highly correlated with one another, they have different impacts on ecosystem function.

Water level fluctuations and ecosystem attributes

Research on the community-wide impacts of water level fluctuations in lakes is scarce, even among the relatively well-studied Great Lakes of North America. Most research focuses on macrophyte community health (Leira and Cantonati, 2008), which, while critical, is only one component of ecosystem functioning. Seasonal fluctuations in the North American Great Lakes average 0.2–0.6 m (Keough et al., 1999), considerably lower than some of the African lakes studied here (range of 0.3–1.8 m). Research on one of Lake Ontario's wetlands, Cootes Paradise Marsh, suggests that changes in water level have community-wide implications, reaching from plankton to fish (Chow-Fraser et al., 1998). In small lakes located in North America, macroinvertebrate response to water level fluctuations follows the intermediate disturbance hypothesis, with the greatest species richness of macroinvertebrate communities coinciding with years of intermediate water level fluctuations (White et al., 2008).

Of the lakes we studied, those with high interannual fluctuations showed higher rates of primary and overall ecosystem production per unit area than those with lower magnitude fluctuations. Increased interannual water level fluctuations, and the subsequent interactions between aquatic and terrestrial phases in the riparian ecotone, act as a nutrient pump which boosts primary production (McLachlan, 1974; Kolding, 1993a; Karengue and Kolding, 1995; Kolding and van Zwieten, 2012). Increased productivity at the base of the food web propagates to higher trophic levels and is significantly correlated with fisheries productivity of lakes within Africa (Melack, 1976; Kolding and van Zwieten, 2012) and elsewhere (Downing et al., 1990).

Previous studies of African lakes suggest links between fisheries productivity and water level fluctuation magnitude. In Lake Kariba, Zambia/Zimbabwe (Karengue and Kolding, 1995), and Lake Turkana, Kenya (Kolding, 1992; Gownaris et al., 2017), both interannual and seasonal fluctuations are correlated with fisheries productivity. In some systems, water levels and their fluctuations are a stronger predictor of yield than are variables related to fishing effort (Jul-Larsen et al., 2003; Gownaris et al., 2017). Fluctuation magnitude is also significantly correlated with fish yield, fishing effort, and biodiversity across tropical lakes and reservoirs in Africa and Asia (Kolding and van Zwieten, 2012). However, this study did not find a significant relationship between Ecopath-reported catch and water level fluctuations at interannual or seasonal scales. This result is somewhat surprising in light of the significant positive relationships we found between water level fluctuations and primary and overall productivity, but possible explanations include: 1) catches in the Ecopath models represent temporal "snapshots", so they may fail to capture the often highly variable yield of African lake fisheries (Jul-Larsen et al., 2003), 2) catches from African lakes and other inland fisheries are notoriously underestimated in national statistics (Bartley et al., 2015; Fluet-Chouinard et al., 2018), which were used for many of the Ecopath models available, 3) African lake fisheries often focus on small and juvenile fish, which may not be recorded in national statistics (Kolding et al., 2016b; Natugonza et al., 2016).

Underlying the more direct fisheries-related attributes are those that determine species diversity and community structure. Both fish diversity and number of trophic levels decreased as the magnitude of water level fluctuations increased. Our findings support the suggestion that fish diversity is lower in systems that are less stable (Jul-Larsen et al., 2003). Additionally, in systems we defined as "high RLLF" (those above the median; $RLLF_a \geq 2.15$ and $RLLF_s \geq 9.4$), a higher proportion of overall biomass exists in lower trophic levels than in the systems we considered to be "low RLLF", indicating a lower relative biomass of high trophic level predators (Fig. 3a). Thus, the gradient of ecosystem stability represented by RLLF from highly fluctuating (externally driven)

to stable (internally driven) systems seems to follow the general r to K continuum (Jul-Larsen et al., 2003). A greater proportion of biomass existing at higher trophic levels in “low RLLF” vs. “high RLLF” systems is consistent with the negative relationship we found between increasing interannual water level fluctuations and trophic efficiency (Lindeman, 1942; Margalef, 1968), maximum trophic level, and mean trophic level of catch across systems. Similarly, Vander Zanden and Fetzer (2007) found that relatively stable marine systems had, on average, a slightly greater number of trophic levels than did lake systems, and that highly fluctuating stream ecosystems had the shortest food chains of all.

Water level fluctuations and ecosystem maturity and stability

The relationships among ecological disturbance, stability, and ecosystem maturity and the cause-effect nature of these relationships are complex and obscure (Orians, 1975; Kolding, 1997; Kolding and van Zwieten, 2006). This study highlights the complexity of the relationship between one form of physical disturbance, i.e. water level fluctuations, and ecosystem maturity. Some of the ecological attributes examined were related to increasing RLLF in the opposite direction of that expected with increasing maturity (Odum, 1969). However, others show no trend with increasing RLLF or the same trend expected with increasing maturity (Table 1). For example, while seasonal fluctuations were negatively correlated with ecosystem stability as measured by Schrödinger's Ratio (R/B ratio: Odum, 1969), this attribute was positively correlated with interannual fluctuations.

Across the systems in this study primary production, total production, and overall standing biomass increased with the magnitude of water level fluctuations. The positive relationship between seasonal water level fluctuations and overall standing biomass was unexpected, as standing biomass generally increases as an ecosystem matures (Odum, 1969; Christensen, 1995). However, a greater proportion of the total system biomass occurred at lower trophic levels in the systems we defined as highly fluctuating (“high RLLF”) than in those we defined as more stable (“low RLLF”), in agreement with Kolding et al. (2016a). Thus, total standing biomass may not be a sufficient indicator of system maturity in lakes and instead should be considered in relation to its distribution along trophic levels, or as the slope of the community biomass-size spectrum (Kolding and van Zwieten, 2006, 2014).

Despite the large body of literature that already exists, better understanding is still needed to determine the relationships among disturbance, stability, and maturity. For example, system stability influences the biological turnover rates of organisms and their response to disturbance (Kolding and van Zwieten, 2012, 2014). Thus, disturbance in the form of changes in water level fluctuation magnitude is likely to have different implications for systems that are relatively stable and mature (e.g. Lake Tanganyika) than those that are relatively unstable and less mature (e.g. Lake Nakuru). Studies conducted within a system over time are likely to prove most useful in understanding the impacts of water level fluctuations on ecosystem functioning. For example, Kolding (1993b) examined the influence of changes in water level for Lake Turkana, Kenya and found that the lake's community structure changed substantially from 1973 (relatively high lake level) to 1987 (relatively low lake level), including a shift in importance from bottom-up to top-down drivers (Kolding, 1993b). In a meta-analysis, Christensen (1995) calculated a higher maturity score, based on seven of Odum's attributes, in the 1973 model than in the 1987 model.

Our results highlight the importance of temporal scale when considering water level fluctuation impacts, as fluctuations at interannual and seasonal scales did not influence the same ecosystem attributes. Species can more easily adapt to predictable disturbance, such as seasonal floods, than to unpredictable disturbance, such as the occurrence of an anomalous flood (Junk et al., 1989; Wantzen et al., 2008a). This “tenet” of the Floodpulse Concept for lakes (Wantzen et al., 2008a) is likely to be particularly true for organisms that are long-lived or exhibit

other K -selected traits (e.g. Ponge, 2013). Importantly, the literature on impacts of water level fluctuations on large, high trophic level organisms (e.g. predatory fish, birds, and mammals) is notably sparse, as reviewed by Leira and Cantonati (2008).

Limitations of our approach

The limitations of the Ecopath modeling suite have been outlined by several other sources (e.g. Christensen and Walters, 2004; Ainsworth and Walters, 2015). As with any model, the quality of a given Ecopath model is highly dependent on the resolution and accuracy of the input data. The models available for this study had pedigree index scores of mid-range quality, between 0.41 and 0.72. These pedigree values reflect the fact that many of the models included in this study relied heavily on empirical relationships, approximations, low precision sampling, and/or Ecopath estimation for select key input values. We readily acknowledge that there exists a variety of data-deficiencies when modeling inland African lakes (Musiguzi et al., 2017), but the models used here represent the best available information in a comparable format. We hope that our study and others (Musiguzi et al., 2017) motivate the construction of African lake ecosystem models that are based on higher quality data and are updated to the current state of these systems. The temporal mismatch between the lake level data and some of the Ecopath models included may have influenced our findings, but we consider this limitation to be minor given the strong correlation we found between water level fluctuations in recent decades and those at longer time scales.

Model quality may relate to the resilience of an ecosystem to perturbation, as found in simulations with 50 Ecopath models, some of which overlapped with those used in this study (Morissette, 2007). However, we found no relationship between a model's pedigree index, number of model groups, or number of trophic links and water level fluctuations, suggesting that model development decisions did not confound relationships between fluctuations and ecological attributes. In addition, our goal was not to explore all factors relating to ecosystem maturity and stability, but to examine whether the African lake ecosystems studied were influenced and possibly driven by water level fluctuations. Some fish-eating trophic groups, including crocodiles, mammals, and birds, were not included in many of the models of study. Where they were present, however, including birds in our calculation of maximum trophic level did not influence our results.

Our statistical approach was carefully chosen to reduce the impact of confounding physical predictors, but it is important to note that the systems studied are highly diverse in most physical characteristics. We did not take all potential physical predictors (e.g. water temperature, mixing patterns) into account, but focused on those that are readily available and often used to categorize lakes. One important consideration in future studies is how lake morphology modulates the influence of water level fluctuations (Wantzen et al., 2008a). For example, the hypsometric curves of Lakes Victoria and Turkana indicate that they exist in pan-shaped basins, while Lakes Naivasha, Awassa, and Nakuru exist in graben-shaped basins (Olaka et al., 2010). Due to their steepness, graben-shaped systems respond to climate fluctuations with greater changes in lake level in relation to surface area as compared to pan-shaped systems (Olaka et al., 2010).

Furthermore, we limited our exploration of perturbation to water level fluctuations at seasonal and interannual scales, but several of the systems of interest (e.g. Lake Turkana) show extreme fluctuations at longer scales (Kolding, 1992), and we did not take system age into account. For example, Lake Kariba, the only reservoir included in this study, was created in 1958 and has thus existed for a much shorter time than the natural lakes considered. We also note that mean depth, which was used to calculate relative lake level fluctuations, is of different descriptive value in shallow systems than in deep ones, where much of the biodiversity may exist in upper zones (e.g. Lake Tanganyika becomes anoxic below the top 100–200 m; De Wever et al., 2005).

Lastly, we recognize that anthropogenic impacts on African lakes, including eutrophication, fishing and invasive species introductions (e.g. Ogutu-Othwayo and Balirwa, 2006; Kolding et al., 2008; van Zwieten et al., 2015), affect their functioning and successive development. For example, Christensen (1995) found that a reduction in fish stocks led to a decreased ecosystem maturity score, as measured based on seven of Odum's attributes, in Lake Tanganyika from 1975 to 1981. Anthropogenic impacts, however, have not been limited to a specific type of system. For example, Lake Kivu (a system we categorized as "low RLLF") and Lake Kariba (a system we categorized as "high RLLF") have both been subject to several introductions of non-native species, some of which have been introduced to both systems (e.g. Lake Tanganyika sardine, *Limnothrissa miodon* and Longfin tilapia, *Oreochromis macrochir*: Froese and Pauly, 2015).

Despite the various limitations and highly varied system resolution and complexity, we found significant relationships between water level fluctuations and several ecosystem attributes. The ability of these trends to stand out regardless of unrelated system and model disparities highlight the importance of water levels fluctuations as drivers of ecosystem structure and function in freshwater systems globally. Regardless, there is still much to be learned about how water level fluctuations affect ecosystem-wide processes in lakes in Africa and elsewhere. Temporal within-system studies, for example, provide important insight into these relationships because they are not subject to the cross-system differences faced by this study. Our findings act as a starting point and highlight the need for more studies that examine ecosystem-level attributes in this context.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jglr.2018.08.005>.

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