

Chemical kinetics control global lake ecosystem responses to climate change

By

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A dissertation submitted in partial fulfillment of
the requirements for the degree of

Doctor of Philosophy
(Freshwater and Marine Sciences)

at the

UNIVERSITY OF WISCONSIN-MADISON

2015

Date of oral examination: 8/24/2015

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Acknowledgements

This dissertation would not have been possible without the support of my friends, family, mentors, and colleagues. My advisor, Pete McIntyre, was instrumental in the formulation and development of the content of this document. I am deeply grateful for his support along with that of the rest of my committee—Paul Hanson, Galen McKinley, Katherine McMahon, Emily Stanley, and Yvonne Vadeboncoeur.

The McIntyre-Peckarsky research group has been an important source of inspiration and feedback during my time in graduate school. Members of the research group have been immensely helpful for me in sorting through my ideas about teaching, collaborating, and research over the last 5 years. It has been fun to grow up alongside the research group itself, and I am very grateful for the opportunity to participate in its development.

Thanks so much to Ellen Hamann for being an awesome field buddy and pop song chanteuse. Thanks to Ellen, the following things will always remind me of being on a boat with her on Lake Tanganyika: the movie *Aliens*, turkey basters, National Public Radio, revenge dreams, the use of undergarments as a sunshade, and Tommy guns. On a related note, thank you to National Public Radio for providing both Ellen and I with hours of fantastic programming while in the field.

I also appreciate the contributions of the other members of the Lake Tanganyika Ecosystem Project (LTEP) field team. Thanks especially to Sam Drerup, Renalda Munubi, Lesley Kim, and Cortney Morris. Dive expert and fish specialist, George Kazumbe was a key member of the LTEP field team. I had substantial field and logistical support from George along

with other members of the Kazumbe family. I would also like to thank the Belgians along with members of the Maendeleo and Bangwe communities for their field assistance and friendship.

Rashid Tamatamah and Mupape Mukuli were helpful in navigating the immigration and research permitting processes in Tanzania. Thank you so much for your help and support. Field work in Tanzania was also facilitated by our hosts at the Tanzania Fisheries Research Institute (TAFIRI) in Kigoma, Tanzania. Thanks to Ismael Kimerei, Hagai John, Huruma Mgana, Prisca Mziray, and others from TAFIRI for being gracious hosts.

There are several undergraduate assistants that I have had the delight of mentoring and advising over the last 5 years. Their efforts contributed substantially to this dissertation. Thanks to undergraduate assistants Vanessa Constant, Melanie Kohls, Nicole Lukens, and Rob Stupar for their hard work.

I would also like to extend a big thank you to the Global Lake Ecological Observatory Network (GLEON). My involvement with GLEON taught me how to be a better data steward and has helped me expand the reach of my work. I have developed a strong sense of shared values with GLEON and I hope to call myself a GLEONite for the rest of my career. All of the chapters in my dissertation reflect the work of my collaborators and co-authors, many of whom I met through GLEON.

I have been heavily influenced and inspired by several charismatic science teachers over the past two decades. Thanks to Jerry Wilkes, Dawn Norton, Jodi Sedlock, Marcia Bjornerud, Bart De Stasio, John Greenler, and Robin Greenler. You helped me build the skills and confidence I needed to start this dissertation in the first place.

And of course, a big thanks to my friends and family that helped celebrate the achievements along the way and helped me get past the rough patches. Thanks to my housemates—Megan, Clare, and Sara, for always being willing to lend an ear. Juma na Uwezo--ninakushukuru sana. Thanks to my parents and step parents—Cindy Johnson, John Kraemer, Damaris Olsen, and Don Johnson for your love. Thanks to Catalina Munteanu for...everything.

Abstract

Myriad patterns and processes at virtually all levels of chemistry, geology, and biology have been observed to depend on temperature. Temperature dependence in nature can often be traced back to the chemical kinetics that underlie all chemical and biochemical reactions. The ubiquity of temperature dependence is central to concerns about the impact of climate change on the Earth. Understanding and predicting responses to climate change requires knowledge of how global patterns of warming rates intersect with the temperature sensitivity of ecosystem processes to elicit ecosystem responses. Here we use long-term temperature data from lakes around the world to assess global patterns in lake warming rates and the sensitivity of lake ecosystems to warming. We find that for many responses to warming, tropical lake ecosystems may be more sensitive than lakes at higher latitudes. Even though tropical lakes tend to have slower surface warming rates, their heightened sensitivity to temperature can cause greater absolute responses to climate warming. We use field data from Lake Tanganyika, the deepest and oldest lake in Africa, to show how the inherent high sensitivity of tropical lakes to warming can lead to complex responses to temperature. In sum, this dissertation highlights the usefulness of chemical kinetics for understanding and predicting global lake ecosystem responses to climate change.

Introduction

“It’s getting hot in herre [*sic*].”

-Nelly

Temperature is often considered a “master” variable in the natural sciences. Observations of temperature dependence in nature have been described for myriad patterns and processes at virtually all levels of chemistry, geology, and biology. Temperature has been attributed with governing everything from the speed of sound (Del Grosso, 1972) to the dissolution rate of cane sugar in water (Arrhenius, 1889) to the rate at which a cricket chirps (Martin *et al.*, 2011). Recent meta-analyses have even shown that temperature governs the configurations of biodiversity across the planet (Allen *et al.*, 2002), and the algal stoichiometry of the global oceans (Yvon-Durocher *et al.*, 2015).

The temperature dependence of patterns in nature can often be traced back to the temperature dependence of chemical kinetics that underlie all chemical and biochemical reactions. The power of chemical kinetics for understanding patterns in nature is a central tenant of the metabolic theory of ecology. Metabolic ecologists have attempted to use mass and temperature scaling of metabolism to provide a unified theory for the importance of organismal metabolism as a driver of ecological dynamics. Since the foundational papers in metabolic ecology were published (Gillooly *et al.*, 2001; Allen *et al.*, 2002; Brown *et al.*, 2004), this sub-field of ecology has grown substantially with thousands of new publications every year. It is one of few branches of ecology that directly links individuals, populations, communities, and ecosystems to fundamental thermodynamics, and its applications are rapidly expanding.

Metabolic ecology has gained prominence, in part, for its capacity to explain and predict the influences of climate change on the earth. The direct, kinetic influence of climate warming is

widely predicted to accelerate metabolism from the cellular to the ecosystem level (Lloyd & Taylor, 1994; Staehr & Sand-Jensen, 2006; Dillon *et al.*, 2010). But with so many physical, chemical, and biological variables in the environment linked to temperature, warming has the potential to have complex, indirect influences on metabolism that outweigh the direct, positive influence. A prominent, recent example being the negative influence of temperature on terrestrial primary production when temperature changes coincide with reductions in precipitation (Zhao & Running, 2010). Thus, to better understand the influences of climate change on metabolism at the global scale, it is important to know how fast ecosystems are warming, how sensitive they are to warming, and how patterns of warming intersect with local temperature sensitivity to produce ecosystem responses to climate change. The aim of this dissertation is to explore all three aspects of the influence of climate change on metabolism with a focus on lake ecosystems. Lake ecosystems were chosen because they are discrete, act as global sentinels of climate change (Adrian *et al.*, 2009), provide key provisioning and cultural ecosystem services to people (Wilson & Carpenter, 1999), and make an important contribution to the global carbon cycle (Tranvik *et al.*, 2009).

While the core of this dissertation focuses on broad scale consequences of warming across lakes, **chapter one** focuses on spatiotemporal variation in warming within a single lake: Lake Tanganyika. As the oldest and deepest lake in Africa with a long temperature record, Lake Tanganyika has been the focus of several studies of climate change impacts on lakes. Thus far, studies of warming trends in Lake Tanganyika have targeted the deep, anoxic zone (> 100 m) where temperature variability primarily reflects long-term climate forcing rather than seasonal variation. Warming trends in the upper water column remain understudied. Here we use a comprehensive database of in situ temperature data that span the lake's lateral extent to explore

spatiotemporal variation in the top 100 m of the water column. Our results demonstrate that century-long warming trends in the upper water column vary by depth, distance from shore, season, and latitude. We explain the observed spatiotemporal variation in warming trends by linking it to vertical mixing patterns within the lake—areas with low vertical mixing experience the fastest warming rates. In sum, chapter one demonstrates that thermal shifts in the upper water column of Lake Tanganyika are in step with climate change and highlights the need to assess variation in warming trends within large lakes.

Vertical stratification patterns in warm tropical lakes, like Lake Tanganyika, may be exceptionally sensitive to surface warming. This heightened sensitivity is due to the nonlinear chemical kinetics underlying the exponential relationship between water temperature and water density. In **chapter two**, I explore whether tropical lake stratification patterns exhibit heightened sensitivity to surface warming using long-term temperature data from 26 lake monitoring sites around the globe. The results show that climate change has altered lake stratification globally and that the magnitude of lake stratification changes are primarily controlled by lake morphometry (mean depth, surface area, and volume) and mean lake temperature. Deep lakes and lakes with high average temperatures have experienced the largest changes in lake stratification even though their surface temperatures tend to be warming more slowly. These results demonstrate that the nonlinear relationship between water density and water temperature and the strong dependence of lake stratification on lake morphometry makes lake warming rates poor predictors of lake stratification responses to warming.

In addition to the exponential relationship between water temperature and water density, the exponential relationship between water temperature and metabolism may also make tropical lakes more sensitive to climate warming. In **chapter three**, I use long-term lake temperature data

from 296 lake monitoring sites around the globe to estimate global patterns in metabolic responses to climate. By substituting temperature data into simple models describing the temperature-dependence of 7 key metabolic rates in lakes (i.e. fish metabolism, gross primary production), I show that most metabolic rates are more sensitive to warming in tropical lakes than lakes at higher latitudes. Our findings indicate that activation energies associated with each metabolic rate provide a simple heuristic for predicting variation in the magnitude and geographic patterns of responses to warming. In many cases, the expected direct effects of warming on lake metabolism are greatest in the tropics.

Chapter four synthesizes concepts from chapter one through three and demonstrates how in Lake Tanganyika, lake stratification responses to climate change outweigh the direct influence of temperature on metabolism. Climate warming is predicted to accelerate lake metabolism due to the fundamentals of biochemical kinetics. But, I show that in Lake Tanganyika, pelagic primary production, pelagic ecosystem respiration, littoral primary production, littoral ecosystem respiration, fish body condition, and some fish species' excretion rates are negatively related to temperature despite the prediction from biochemical kinetics. In Lake Tanganyika, the effects of surface warming on vertical mixing belies the direct, kinetic influence of temperature on metabolism. Negative "apparent" temperature dependence of metabolism may be widely observed in the tropics when vertical mixing is a key source of nutrients to the photic zone. The indirect influences of temperature on metabolism can outweigh the direct influence and should be incorporated into models of lake ecosystem responses to climate change.

In sum, this dissertation partially addresses the three questions that I posed earlier in the introduction as they relate to lake ecosystems: (1) How fast are lake ecosystems warming? (2)

How sensitive are lake ecosystems to warming? and (3) How does warming intersect with local temperature sensitivity to produce lake ecosystem responses to climate change? Most lakes are warming, but warming trends vary substantially within and across lakes. When temperature dependences are nonlinear, as in the case of water density and lake metabolism, warm ecosystems tend to be more sensitive to temperature change. When global patterns in lake warming trends intersect with local lake sensitivity to temperature, the tropics emerge at the forefront of climate change impacts on lake ecosystems.

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Chapter 1: Century-long warming trends in the upper water column of Lake Tanganyika*

Abstract

Lake Tanganyika, the deepest and most voluminous lake in Africa, has warmed over the last century in response to climate change. Separate analyses of surface warming rates estimated from in situ instruments, satellites, and a paleolimnological temperature proxy (TEX₈₆) disagree, leaving uncertainty about the thermal sensitivity of Lake Tanganyika to climate change. Here, we use a comprehensive database of in situ temperature data from the top 100 meters of the water column that span the lake's seasonal range and lateral extent to demonstrate that long-term temperature trends in Lake Tanganyika depend strongly on depth, season, and latitude. The observed spatiotemporal variation in surface warming rates accounts for small differences between warming rate estimates from in situ instruments and satellite data. However, after accounting for spatiotemporal variation in temperature and warming rates, the TEX₈₆ paleolimnological proxy yields lower surface temperatures (1.46 °C lower on average) and faster warming rates (by a factor of three) than in situ measurements. Based on the ecology of Thaumarchaeota (the microbes whose biomolecules are involved with generating the TEX₈₆ proxy), we offer a reinterpretation of the TEX₈₆ data from Lake Tanganyika as the temperature of the low-oxygen zone, rather than of the lake surface temperature as has been suggested previously. Our analyses provide a thorough accounting of spatiotemporal variation in warming

* Published as Kraemer, B. M., S. Hook, T. Huttula, P. Kotilainen, C. M. O'Reilly, A. Peltonen, P.-D. Plisnier, J. Sarvala, R. Tamatamah, Y. Vadeboncoeur, B. Wehrli, and P. B. McIntyre. 2015b. Century-Long Warming Trends in the Upper Water Column of Lake Tanganyika. PLOS ONE 10:e0132490.

rates, offering strong evidence that thermal and ecological shifts observed in this massive tropical lake over the last century are robust and in step with global climate change.

Introduction

Climate change is altering the thermal characteristics of lakes worldwide, leading to a broad range of impacts on ecosystem processes (Adrian et al. 2009). Thermal characteristics of lakes directly influence water column stratification (Livingstone 2003, Coats et al. 2006, MacIntyre 2013), water budgets, oxidation-reduction state (Davison and Seed 1983), greenhouse gas efflux rates (Yvon-Durocher et al. 2012, 2014), and organismal metabolic rates (Gillooly et al. 2001). Despite recognition that climate change has important direct and indirect effects on lake ecosystems, monitoring of long-term thermal changes in lakes remains limited.

Compared with temperate and arctic lakes, long-term, in situ lake temperature data sets are rare in the tropics. Satellite remote sensing of lake surface temperatures can redress the latitudinal bias of temperature monitoring for large lakes. Remote sensing typically yields comparable results to in situ monitoring (Schneider and Hook 2010, MacCallum and Merchant 2014), but is presently limited to only three decades of imagery. Conversely, paleolimnological temperature proxies can expand the temporal scales of lake temperature measurement, but the expense of core collection and analysis limits the spatial scope of this approach. Ideally, assessment programs should simultaneously consider multiple independent methods to cover longer timescales and allow maximal spatial and temporal resolution.

East Africa's Lake Tanganyika has become one of the best-known cases of warming among the world's lakes. As a result of the pattern of warming with depth, the lake has become more stratified, thereby reducing internal nutrient loading to the upper water column (Verburg et

al. 2003, O'Reilly et al. 2003, Verburg and Hecky 2009). Evidence from sediment cores suggests that reduced internal nutrient loading has caused the lake to become less productive, with implications for the lake's fishery (O'Reilly et al. 2003, Tierney et al. 2010) on which hundreds of thousands of people depend for their nutrition and livelihoods.

Multiple methods have independently been used to estimate the warming trends in this large (volume: 18,900 km³), old (~12 million years), and meromictic rift lake. The in situ water temperature record is one of the longest direct observation time series from any lake in the world. While historical temperature data are distributed across the entire spatial extent of the lake, previous analyses have focused on long-term warming trends in deep water (> 100 meters depth) in the north basin (~1/3 of the lake's volume) in the wet season (October-April) where the data are the richest (Verburg et al. 2003, O'Reilly et al. 2003, Verburg and Hecky 2009). Lake surface temperatures have been measured using space-borne radiometers since 1985 including the Advanced Very High Resolution Radiometers (AVHRR) and the Along Track Scanning Radiometer (ATSR) (Schneider and Hook 2010). The high-resolution satellite record (mean data gap is 5.1 days) complements the long-term but sporadic in situ temperature record from Lake Tanganyika. In addition to in situ instruments and satellites, the TEX₈₆ paleotemperature proxy has been used to reconstruct 60,000 years of lake surface temperature data in Lake Tanganyika (Tierney et al. 2008, 2010). The TEX₈₆ paleotemperature proxy uses the temperature dependence of Thaumarchaeal (planktonic microorganisms) glycerol dialkyl glycerol tetraether cyclization to reconstruct surface temperatures (Wuchter et al. 2004, Powers et al. 2004).

Published warming rate estimates from each method disagree by a factor of two. In situ instruments, the TEX₈₆ paleolimnological proxy, and satellite-borne radiometers reporting warming rates of 0.15 (Schneider and Hook 2010), 0.21 (Tierney et al. 2010), and 0.30 °C

decade⁻¹ (Schneider and Hook 2010), respectively. This variation in temperature trend estimates could be attributable to spatiotemporal variation in warming rates because they were applied to different parts of the lake, different portions of the year, and different lengths of time. However, spatiotemporal variation in warming trends have not been explored in lake Tanganyika. The differences might also be attributable to inherent differences between the measurement approaches themselves (e.g. temperature at the air-water interface measured by satellites versus bulk surface temperatures measured by in situ thermometers). Our understanding of the impacts of warmer temperatures on Lake Tanganyika's spectacular ecosystem would benefit from the reconciliation of all three perspectives to yield a more consistent estimate of warming rates.

In this paper, we assess whether warming rates in the upper water column (<100 m depth) vary spatially within the lake using in situ data and test whether spatiotemporal variation in temperature and warming rates can account for observed differences between measurement methods. To address these goals, we synthesized new and previously published in situ surface temperature data with other data sources (the TEX₈₆ paleolimnological temperature proxy, the ATSR satellite instruments, and the AVHRR satellite instruments) for Lake Tanganyika. Using the in situ data, we develop models to characterize spatiotemporal variation in upper water column temperatures and rigorously compare model output to the other data sources. Our work demonstrates the need to explore spatial variation in the response of lake temperature to climate change within large lakes.

Methods

Study Location

Lake Tanganyika is a long (650 km) and deep (1470 m) lake located in East Africa and oriented on a roughly north-south axis between 3.4 and 8.9 °S latitude (Fig. 1). It has three basins that are separated by relatively shallow transverse sills (~500 m depth). The north, central, and south basins are located between 3.4-5.8 °S, 5.8-7.0 °S, and 7.0-8.9 °S, respectively. The south basin is the deepest while the north basin has the highest volume. Seasonal southeast trade winds during the dry windy season (May-October) and differential evaporative cooling over the 650 km length of the lake drives large scale convective circulation and internal waves with a period of 25 to 30 days (Verburg et al. 2011). The internal waves are reactivated at the end of the dry season (September) and persists through the rest of the year with decreased amplitude (Podsetchine and Huttula 1996, Plisnier et al. 1999, Verburg et al. 2011).

Temperature Data

Several syntheses of in situ temperature data have been published for Lake Tanganyika (Verburg et al. 2003, O'Reilly et al. 2003, Verburg and Hecky 2009). These syntheses focused on deep water below 100 meters depth. Here we expand upon those records by including historical temperature data sets that were not included in previous work and by focusing on temperature in the upper water column (Appendix 1). This enabled us to include data which span the spatial extent of the lake and the entire seasonal range. We also include new temperature data in the north, central, and south basins (Appendix 1) that were collected near Kigoma, Mpulungu, and offshore from Tanzania's Mahale Mountains National Park. Field research permits were granted by the Vice Chancellor of the University of Dar es Salaam. We collected these data between 1993-2013 using an YSI 6600 V2 data sonde, titanium RBRduo TD, Seacat Profiler V3.1b, and Onset HOBO U22 temperature loggers that were cross calibrated biannually. Temperature data taken before 1993 were measured using data loggers, standard mercury

thermometers, and reversing thermometers. All temperature data taken over the last century reported here come from at least 1.5 km offshore and where the water depth exceeds at least 100 m. Much of the data come from sites near the three major research centers on the lake near Uvira, Democratic Republic of Congo; Kigoma, Tanzania; and Mpulungu, Zambia (Fig. 1). In total, 13985 temperature observations were included in our analysis. The temperature data used here are freely available through the Long-Term Ecological Research network data portal (Kraemer et al. 2015).

TEX₈₆ is a well-documented surface water temperature proxy applied to the open ocean and many large lakes that have well-preserved sediments with limited inputs of terrestrial organic matter (Tierney et al. 2010). Sediment cores from Lake Tanganyika were taken from the central basin of the lake at 6.552 °S, 29.975 °E (Fig. 1) (Tierney et al. 2010). The original published TEX₈₆ data (Tierney et al. 2008) were recalibrated and updated in a subsequent publication (Tierney et al. 2010). The recalibration leads to a downward temperature correction of about 2.0 °C. All data presented here are based on the updated calibration procedure. Uncertainty in the TEX₈₆ temperature estimates arises from random error in the calibration and aging of the sediment core, but results are considered to be accurate to within 0.4°C for Tanganyika (Tierney et al. 2010). In total, 9 TEX₈₆ temperature observations over the last century are included in our analysis, each interpreted as the mean annual surface temperature at the core site. The complete TEX₈₆ temperature data used here are freely available through the World Data Center for Paleoclimatology (Tierney et al. 2010).

Calibrated satellite lake skin temperature data for Lake Tanganyika spanning the seasonal range have been published in an online database for a single data extraction point in the central basin (Schneider and Hook 2010). We update these published data with the addition of two years

of data (2010-2011) processed by the same methods. The ATSR and AVHRR data used in this study were acquired for the periods when they were available from 1985-2011, and excluded pixels with cloud cover following the algorithms of previously published work (Schneider and Hook 2010). Night-time ATSR and AVHRR data were extracted and averaged within a 3 X 3 km and 4 X 4 km area, respectively, centered over the location 6.792°S, 30.072 °E in the central basin of the lake (Fig. 1). Night-time data were used to avoid bias from orbital drift of the satellites. Satellite temperature estimates were calibrated and validated against buoy data from the Laurentian Great Lakes (Schneider and Hook 2010). The mean and maximum data gaps for the Lake Tanganyika satellite data are 5.1 days and 112 days, respectively. The satellite data are freely available through the “Large Lakes” data portal on the National Aeronautics and Space Administration’s Jet Propulsion Laboratory website (Schneider and Hook 2010).

Statistical modeling of in situ temperature

We developed a statistical model of in situ temperatures to (1) test whether upper water column (top 100 meters) warming rates vary spatiotemporally, and (2) determine whether differences in the location and time of satellite and TEX_{86} measurements can account for disparities in temperature and warming rates among these three methods. The spatial and temporal incompleteness of Lake Tanganyika’s in situ temperature data precluded traditional statistical modeling such as autoregressive integrated moving average (ARIMA) approaches. Instead, we build a series of general linear mixed effects models to all available temperature observations in the upper water column (≤ 100 m depth) made over the last century. We fit the model separately for data from 11 depths (0, 10, 20, 30, 40, 50, 60, 70, 80, 90, and 100) in the upper water column. The structure of the model reflects known and hypothesized drivers of temperature variation in the upper water column of Lake Tanganyika:

$$Y_{i,w} = L_w + S_w + \beta_1 Decade + \beta_2 GISS + \beta_3 Decade * L + \beta_4 Decade * S + \beta_7 Decade * H_w + \epsilon_i$$

where $Y_{i,w}$ is the i th temperature observation on the w th week of the year; L_w is the week of the year-specific effect of latitude ($^{\circ}$ S); S_w is the week of the year-specific effect of distance from shore (km); *Decade* is the decimal decade of each observation since 1900; *GISS* is the detrended Goddard Institute for Space Studies Land-Ocean Temperature Index (GISS) (Hansen et al. 2010); L and S are the latitude and distance to shore at the location of each measurement; H_w is the average relative percent humidity for the week of the year when the temperature measurement was made (averaged over a 2.5 year period from 2011-2013 from a weather station in Kigoma, Tanzania); and ϵ_i is the observation-specific error. In total, the models characterizes spatial, seasonal, interannual, and century-long variation in temperature.

The term in the model for latitude (L_w) and distance to shore (S_w) at the location of each measurement characterize spatial variation in temperature over the course of the year (but not inter-annual or century-long variation). L_w and S_w were fit separately for each week of the year because these effects are known to vary substantially within a season. In other words, L_w , and S_w are interaction terms between week of the year (as a random effect) and two spatial predictors of temperature (L , S).

The β terms in the above equation are coefficients for the continuous, fixed effects in the model that characterize inter-annual and century-long variation in temperature. In part, this variation is captured by the first two fixed effects in the model; *Decade* and *GISS*. β_1 , the coefficient for the *Decade* term, can be interpreted as the generalized, century-long warming rate. β_2 , the coefficient for the *GISS* term, can be interpreted as the influence of global, inter-

annual variation in temperature on upper water column temperatures in Lake Tanganyika. We include the detrended, monthly GISS index over the period from 1912-2013 as a predictor because inter-annual variation in Lake Tanganyika temperatures have been shown to closely track global air temperatures (Verburg and Hecky 2009). The GISS data have had the long-term trend removed so that the GISS coefficient (β_2) describes the effect of interannual variation in global land surface temperatures but not the long-term warming trend.

The long-term warming trend has also been hypothesized to vary seasonally and spatially within the lake (Verburg and Hecky 2009). The continuous, fixed interaction terms in the model between *Decade* and latitude (L); *Decade* and distance from shore (S); and between *Decade* and the average relative humidity for week of the year (H_w) characterize the influence of location within the lake and season on the long-term temperature trend. The average relative humidity on each week of the year was included in the model as an interaction term with *Decade* because humidity is tightly related to the multivariate seasonal axis from the cold, dry and windy season to the hot, wet, and less windy season. The β terms associated with these interaction terms (β_3 , β_4 , and β_5) can be interpreted as the impact of L , S , and H on the generalized warming rate estimate (β_1).

To assess the accuracy of the model, we compare raw temperature measurements to modeled estimates using the root mean squared error (RMSE) from ordinary least squares regression. We used bootstrapping to minimize spatial and temporal autocorrelation in the temperature data; we randomly sample 10% of the temperature observations made over the last century for each 10 meter depth bin and fit the model to that subset of the data. We repeated this procedure 100 times with replacement and examined the distribution of each model parameter across models. By randomly subsetting the data across large spatial and temporal scales, we

severely limit violations of the assumption that temperature data are not spatially or temporally autocorrelated. To interpret the robustness of our model, we compare the coefficients from the full model to the distribution of parameters derived from fitting data subsets. Because the median parameter is more robust to the violations of model assumptions, the median parameters from model subsets are used for predicting in situ temperature data at the sites of the satellite and TEX₈₆ core extractions.

In situ temperature comparison to TEX₈₆ and satellites

The second major goal of the in situ temperature model was to determine whether the observed variation in warming rates based on in situ temperature data can account for differences in warming rate estimates across methods (in situ, satellites, TEX₈₆). Ideally, TEX₈₆ temperature data and satellite data could be compared directly to in situ temperature observations made in the same location. However, that is not possible with the available data. Instead, we used output from the in situ temperature model to predict surface temperatures at the satellite data extraction site and the TEX₈₆ core site over time. First, we substituted the latitude (6.55° S) and distance from shore (5.62 km) at the location of the TEX₈₆ core site into the temperature model fit to surface temperature data to generate daily estimates of surface temperature at the core site. We used the daily estimates of modeled, in situ surface temperature to calculate annual means for comparison to the raw TEX₈₆ data. Similarly, we substituted the latitude (6.72° S) and distance from shore (30.69 km) at the location of the satellite extraction site into the temperature model to generate daily estimates of surface temperature at the site of the satellite extraction. The resulting model output is our best estimate of surface temperatures at those specific locations, and is informed by all available in situ data.

Temperature model output for the locations of the satellite extraction and the TEX₈₆ core site were compared to raw data from each method using major axis (MA) regression. MA is a type II, least squares regression technique used when there is error in the measurements of both x and y variables (McArdle 1988). The long-term warming rates associated with modeled in situ data, satellites and TEX₈₆ were based on annual means. To estimate the surface warming rate based on TEX₈₆ temperature data, we randomly resampled from the TEX₈₆ error distribution (± 0.4 °C) (Tierney et al. 2010) to account for uncertainty in the TEX₈₆ calibration procedure. We used the resampled data to calculate the long-term trend. We repeated this resampling procedure 1000 times to estimate a distribution of warming rate estimates and an associated 95% confidence interval. Warming rates were compared using analysis of covariance (ANCOVA). All statistics were computed using R (R v3.1.0, core team, 2013).

Results

Statistical modeling of in situ temperature

The models fit to in situ temperature observations in the upper water column of Lake Tanganyika accounted for 44-89% of the variation in temperature depending on the depth to which the model was fit (Appendix 2). The fixed effects in the models which characterize inter-annual and century-long temperature trends explained progressively more of the temperature variation with increasing depth. The fixed effects explained 4% of the variation in surface temperature while they explained 45% at 100 m (Appendix 2). The RMSE of the temperature models decreased with depth from 1.19 °C at the surface, to 0.21 °C at 100 m (Appendix 2). Model residuals were normally distributed and unrelated to any of the predictors in the model.

The random effects of latitude ($^{\circ}\text{S}$) and distance to shore (km) on temperature varied over the course of the year. Latitude showed strong seasonal variation in its impact on temperature. As expected, during the dry season, temperature increased with latitude and during the wet season temperature decreased with latitude. The distance from shore had a weak, seasonally variable impact on temperature; in the dry season, temperature tends to decrease with distance from shore and in the wet season temperature tends to increase with distance from shore. Surface temperatures were strongly related to the GISS-LOTI, but this relationship was less pronounced at depth and became slightly negative below 70 m (Appendix 3).

According to the model of in situ temperatures, the surface of the lake has warmed on average at a rate of $0.129 \pm 0.023 \text{ }^{\circ}\text{C decade}^{-1}$ over the period 1912-2013. Water temperatures increased over the period 1912-2013 at all depths from 0-100 m across the spatial extent of the lake (Fig. 2). The fastest warming rates on average can be found at depths of 50-80 m (Fig. 2). The model results suggest that there is significant variation in warming rates over the surface of the lake and through the year. On average, warming rates at the northern tip of Lake Tanganyika exceed warming rates at the southern tip by about $0.013 \text{ }^{\circ}\text{C decade}^{-1}$ (Fig. 2). This latitudinal difference is most pronounced at 50 m below the surface where the northern basin is warming $0.076 \text{ }^{\circ}\text{C decade}^{-1}$ faster than the southern tip of the lake (Fig. 2). The seasonal temperature cycle also influences the rate of temperature change. Surface warming rates vary by $0.080 \text{ }^{\circ}\text{C decade}^{-1}$ over the seasonal cycle with the slowest surface warming rates occurring in the dry season when temperatures are typically lower (Fig. 2). The opposite pattern (warming rate faster in dry season) is observed over the depth range from 20–80 m (Fig. 2). The distance from shore also impacted the century-long warming rate but the effect was weaker than the effects of latitude and seasonality. The fastest surface warming rates occurred close to shore but for much of the water

column (10-50 m and from 90-100 m), distance to shore was negatively related to warming rate (Fig. 2).

Overall, the model coefficients for the full fitted model agreed well with the median coefficients from models fit to resampled 10% subsets of all data (Appendix 3). However, the full model tended to underestimate the effect of latitude and seasonality on warming rates, and overestimate the generalized warming rate and the effect of GISS-LOTI on temperature data (Appendix 3). The semi-parametric data subsetting approach is more robust than the full model which makes more assumptions about the underlying data. However, if the full model is more accurate, then the seasonal and latitudinal variation in warming rates estimated here may be overestimated.

In situ temperature comparison to TEX_{86} and satellites

Between 1985 and 2011, satellite temperatures were 0.26°C colder on average than the modeled in situ surface temperatures. Despite the difference in temperatures, there was no significant difference in surface warming rates between satellite data ($0.225 \pm 0.112^{\circ}\text{C decade}^{-1}$) and modelled in situ data ($0.164 \pm 0.075^{\circ}\text{C decade}^{-1}$) over the period from 1985-2011 (analysis of covariance, $p = 0.26$, Figs. 3-5). The relationship between daily modeled in situ surface temperature (x axis) and satellite temperature (y axis) had a slope significantly greater than one (slope = 1.11, 95% confidence interval = 1.07-1.15, MA regression with 100 permutations, Fig. 3). The slope of the annual averages of modeled in situ surface temperature (x axis) versus satellite temperature (y axis) was significantly greater than one (slope = 2.12, 95% confidence interval = 1.55-3.14, MA regression with 100 permutations, Fig. 3).

TEX₈₆-based temperatures were 1.46 °C colder on average than the modeled in situ surface temperatures (Fig. 3). TEX₈₆-based warming rates were faster than in situ temperatures by a factor of 3 over the period from 1918 to 1996 (0.248 ± 0.053 °C decade⁻¹ for TEX₈₆ versus 0.079 ± 0.052 °C decade⁻¹ for modeled in situ data, Fig. 4). After accounting for uncertainty in the TEX₈₆ temperature calibration using monte carlo simulations with 100 permutations, there was still a significant difference in warming rates between TEX₈₆ and the modeled in situ temperature trend (analysis of covariance $p < 0.01$, Figs. 4 and 6). The slope between annual modeled in situ surface temperature (x axis) and TEX₈₆ temperature (y axis) was significantly greater than one (slope = 5.29, 95% confidence interval = 2.96-20.91, MA regression with 100 permutations, Fig. 4).

Discussion

All three methods (in situ, satellite, TEX₈₆) suggest that the surface of Lake Tanganyika warmed significantly over the last century (linear regression, $p < 0.05$, Figs 4-6). Our analyses provide a detailed portrait of spatiotemporal patterns of warming in the upper water column of Lake Tanganyika, revealing that previous work on long-term warming in deeper water capture only a portion of the changes over the last century. Spatial variation in warming rates partially account for the differences between warming rate estimates based on in situ, satellite and TEX₈₆ data. However, even after accounting for spatiotemporal variation in temperature and warming trends, key differences among methods remain.

Spatiotemporal variation in warming rates appears to be linked to vertical mixing patterns within the lake. Warming rates tend to be slower in areas of the lake with relatively high vertical mixing. For instance, warming rates are slower in the southern latitudes where vertical mixing is

greater. The most persistent vertical mixing in the southern basin occurs in the dry windy season when wind-induced tilting of the thermocline induces 'primary upwelling' as the thermocline is lifted toward the surface there. Primary upwelling may slow apparent surface warming rates by transporting accumulated surface heat to deeper water and refreshing the surface with cold hypolimnetic water annually. Thus, in effect surface heat is distributed into a much larger mass of water than the local epilimnion, yielding a slower warming rate in the upper water column. Enhanced vertical mixing has also been suggested as a mechanism for slower warming in the upper water column at the onset of summer in Lake Ontario (Finlay et al. 2001). Areas of Lake Ontario that were more strongly stratified warmed faster at the surface than areas with lower stratification (Finlay et al. 2001). A similar pattern was observed in Lake Tanganyika but over interannual timescales instead of over seasonal timescales.

Seasonal differences in the pattern of warming with depth also suggest that warming rates are linked to patterns of vertical mixing. Surface warming rates in the wet season were faster than warming rates from 10-100 m whereas surface warming in the dry season is slower than at depth. This pattern can be explained by seasonal differences in the strength of microstratification at the surface of the lake. Due to weakening of surface winds in the wet season, a secondary thermocline typically forms in the top 5-15 meters of the water column in Lake Tanganyika (Verburg and Hecky 2003). The secondary thermocline serves as a barrier to mixing and may prevent the transfer of heat to deeper depths in the wet season. Heat that gets trapped in the top 5-15 m of the water column above the secondary thermocline may be lost back to the atmosphere through outgoing long wave radiation, sensible heat loss, or latent heat loss. However, latent heat losses may be relatively small in the wet season due to high humidity and low wind speeds. In the dry season, persistent trade winds disrupt the secondary thermocline, thus heat may be

transferred to greater depths at that time of year. Thus seasonal variation in surface microstratification may explain season differences in the pattern of warming with depth.

Periodic, localized vertical mixing also occurs in near shore areas of Lake Tanganyika when internal waves interact with the lake bottom (Corman et al. 2010). Turbulent mixing of this sort is likely to transmit heat from the surface to deeper parts of the lake, thereby slowing apparent surface warming rates near shore. The coefficient in our model associated with the interaction term between distance to shore and *Decade* suggested that warming rates may be slower nearshore only at the surface and from 60-80 m depth. Thus our model does not strongly support the hypothesis that warming rates closer to shore at the surface are slower than warming rates over deeper water where internal waves interact less strongly with the lake bottom. We may not have detected a strong effect of distance from shore on warming rates because we excluded data that were taken from areas shallower than 100 m and less than 1.5 km from shore.

The in situ temperature model suggests that the northern basin of the lake is warmer on average and experiencing relatively fast surface warming rates. This result contrasts with the global latitudinal gradient in lake warming where temperature is negatively correlated to warming rates (Schneider and Hook 2010). The warmest time of year in Lake Tanganyika (wet season) has the fastest surface warming rates. At the global scale, warming is often slower at times of the year when temperatures are high (Screen and Simmonds 2010), which also contrasts with our finding that water temperatures in the warm, wet season are warming faster.

In situ temperature comparison to satellites

The difference between satellite and modelled in situ temperatures is at least partly attributable to differences in the time of day when satellite and in situ data are collected. In situ

temperature data are measured during daylight hours when surface temperatures are at or near daily peaks, whereas satellite data are measured at night to avoid bias from orbital drift of the sensors (Jin and Treadon 2003). At night, surface temperature is typically 0.2-0.6 °C lower than the daytime temperature (Verburg and Hecky 2003). Thus, the average observed temperature difference between satellites and in situ instruments (0.26 °C lower for satellites) could be entirely explained by the timing of observations. Furthermore, the difference between nighttime and daytime surface temperatures are lowest in the cooler dry season when winds disrupt daytime surface microstratification. Similarly, the difference between satellite (night) and in situ (day) temperatures are also smallest in the cooler dry season. This further supports the hypothesis that differences between in situ and satellite-based surface temperature estimates primarily reflect differences in the time of day when temperature is measured by the two methods.

Even after accounting for diurnal variation in surface temperatures, there remains a substantial amount of unexplained variation in the comparison between daily satellite and daily in situ temperatures (Fig. 3). Some of this variation may arise from spatial or temporal biases in satellite data collection. For instance, non-random spatial variation in surface temperature and atmospheric interference (clouds, smoke) could bias satellite temperature measurements (Merchant et al. 2005). Additionally, satellite data represent only cloud-free days, which could bias the annual mean surface temperature estimates toward warmer temperatures. Differences between temperature at the air-water interface (skin temperatures) and bulk surface water temperature may also explain additional variation in the difference between satellite and modeled in situ temperature. For example, satellite-based temperatures often exceed in situ measurements by ~0.2 °C in lakes due to the differences in heat exchange between the

atmosphere and skin water versus surface bulk water (Roni et al. 2013, Wilson et al. 2013, MacCallum and Merchant 2014). While inherent differences in the measurement approaches may be reflected in our data, satellite data and in situ data match relatively closely (Figs. 3 and 4) and the differences between satellite and in situ temperatures observed here likely reflect the time of day when measurements are made.

In situ temperature comparison to TEX₈₆

The substantial differences between TEX₈₆ temperature data and the modeled in situ temperature data at the location of the sediment core raise questions about interpretation of TEX₈₆ data. Based on the pattern of mismatch between in situ bulk temperature and TEX₈₆ temperature (Fig. 6), it appears that the TEX₈₆ paleolimnological proxy substantially and consistently underestimates the surface temperature in Lake Tanganyika using the current TEX₈₆ calibration method. Given the direction of the mismatch, the TEX₈₆ record may be most closely related to temperature at a fixed depth below the surface, or the average temperature over a range of depths (Schouten et al. 2012). The quantitative agreement between TEX₈₆ temperatures and in situ temperatures over the last century is closest for in situ measurements taken at ~60 m depth where temperatures are colder than the surface. However, warming rates inferred from TEX₈₆ are still much greater than those at 60 m according to our in situ temperature model for that depth. Furthermore, the satellite-based temperature data were extracted from images near the site where the sediment core was collected for TEX₈₆ analysis (Fig. 1), yet the satellite-based warming rate is similar to modelled in situ data and far lower than TEX₈₆ temperatures. Together, these comparisons suggest that it is unlikely that warming at the core site was truly 3 times faster than that indicated by in situ data.

We propose an alternative explanation for the mismatch between TEX_{86} and in situ temperature data that is rooted in the ecology of Thaumarchaeota. Though no single abiotic shift is sufficient to explain why TEX_{86} suggests more rapid warming than in situ data in Lake Tanganyika, the observed shallowing of the oxycline suggest that TEX_{86} could reflect a biological response overlaid upon the in situ warming pattern. In Lake Tanganyika, Thaumarchaeota are most productive in the zone of the lake with moderate to low oxygen levels (“suboxic zone,” 0.5-4.0 mg L⁻¹ dissolved oxygen, 40-180 m depth) (Schouten et al. 2012). The suboxic zone has shallowed over the last century due to reduced vertical mixing (Verburg et al. 2003, O’Reilly et al. 2003, Verburg and Hecky 2009, Van Bocxlaer et al. 2012), suggesting that Thaumarchaeota have likely moved into shallower, warmer water. The magnitude of this inferred shift in the depth of Thaumarchaeota is comparable to the upward shift observed in the depth niche of endemic deep water molluscs in response to the shallowing oxic zone in Lake Tanganyika (Verburg and Hecky 2009, Van Bocxlaer et al. 2012). Shallowing of Thaumarchaeota’s oxygen niche would lead to warmer TEX_{86} temperatures over time irrespective of warming rates at any specific depth. Thus, TEX_{86} could be responding to an ecological change that is indirectly linked to the temperature that it purportedly measures (Wuchter et al. 2004, Castañeda and Schouten 2011).

The combination of climate-mediated warming at all depths with upward shifts in the oxygen niche of Thaumarchaeota is sufficient to explain the observed differences in both temperatures and warming rates between methods. If this interpretation is correct, the TEX_{86} paleolimnological proxy is still valid but may be more closely related to the temperature in the suboxic zone, not temperature at the surface or any other fixed depth. As a measure of suboxic zone temperature, the TEX_{86} record augments previous analyses of shallowing trends in snail

depth distributions, and directly connects the measured temperature increases and estimated stabilization of the water column with organismal responses to climate change in Lake Tanganyika. Thus, our reinterpretation of the TEX₈₆ record could lead to a more nuanced view of the entire 60,000 year temperature time series derived from TEX₈₆ data for Lake Tanganyika. Without accounting for this ecological perspective, the most rapid rates of warming and cooling in the TEX₈₆ record may be especially exaggerated, and published temperatures are likely to reflect temperature at a particular depth only during periods of relative stasis in suboxic zone depth.

Conclusions

Our update and synthesis of in situ temperature data from Lake Tanganyika demonstrates that long-term warming rates in Lake Tanganyika vary with latitude, distance from shore, and with the seasonal cycle. Though our statistical approach to the incomplete space-time matrix of in situ observations from Lake Tanganyika has limitations, it nonetheless reveals consistent patterns of spatial variation in warming that illustrate a need to assess the spatial dimensions of warming within large lakes. This variation is most likely driven by variation in vertical mixing; areas and times of year with low vertical mixing experience the fastest warming rates. This pattern may be observed in other large lakes with spatial and temporal variation in vertical mixing patterns. There are few large lakes where time series of in situ observations encompass a wide enough range of locations to estimate spatial variation in warming rates. Such comparisons have been made over shorter time scales in other large lakes, and have revealed substantial differences in warming across the surface of lakes (Austin and Colman 2007, Ngai et al. 2013). The analyses of spatial variation in lake skin temperatures for Lake Tanganyika from satellites could be an informative complement to our work on spatially distributed in situ data.

The broad quantitative agreement between temperature records from satellites and in situ instrumental data engenders new confidence in the records themselves as well as their implications for climate change effects. Unfortunately, there are few lakes in the world that have temperature records from multiple methods spanning over a century of change. Of the lakes that have well-preserved sediments, few also have both long-term in situ temperature records and surface area large enough for unobstructed satellite-based measurements. Lakes Baikal and Malawi could provide all three types of records, thereby broadening perspectives on the effects of climate change on surface temperatures as well as testing whether our reinterpretation of the TEX₈₆ paleolimnological temperature proxy could be correct for other lakes.

As the oxic zone shallows in Lake Tanganyika, aerobic organisms will be forced upward in the water column where temperatures are both warmest already and rising fastest. Higher temperatures exact metabolic costs for these organisms, potentially reducing their discretionary energy available for growth and reproduction (Dillon et al. 2010, Sumaila et al. 2011). Reduced vertical mixing associated with thermal shifts has already diminished internal nutrient loading, leading to reduced primary productivity and shifts in phytoplankton assemblages (Verburg et al. 2003, O'Reilly et al. 2003, Tierney et al. 2010). Warm lakes like Lake Tanganyika are especially vulnerable to warming-driven shifts in lake stratification due to the nonlinear relationship between water density and water temperature. The combination of reduced oxic habitat, increased metabolic demands, and lower primary productivity is likely to have negative effects on the lake's ecosystem and the hundreds of thousands of people who depend on the lake for their nutrition and livelihoods.

Acknowledgements

The data presented here represent the hard work of hundreds of scientists, technicians, and students who have measured temperature over the last century in Lake Tanganyika. Logistical support was provided by the Tanzanian Fisheries Research Institute. Research permission was provided by the University of Dar es Salaam. Thanks to Lieselot De Reydt, Maarten Tierens, Sarah Verniers and Moritz Rahlfs for translating the text accompanying historical temperature data, and anonymous reviewers for constructive suggestions. Thanks to Catalina Munteanu for her support and suggestions.

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Figures

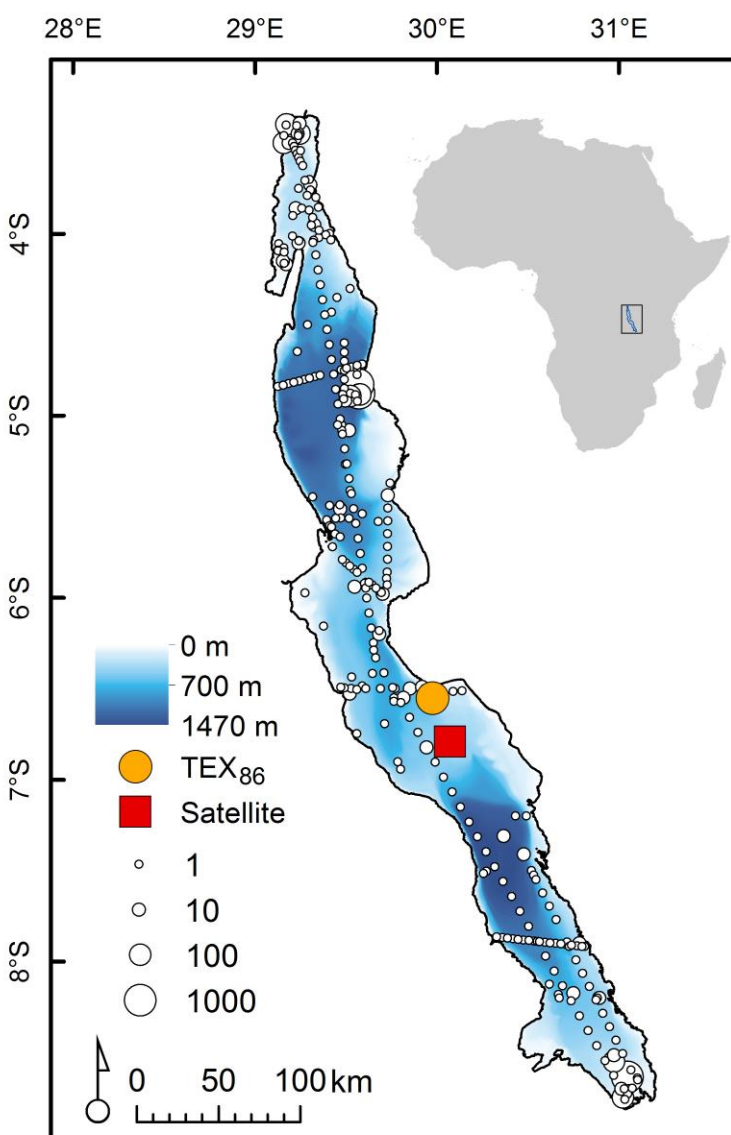


Fig. 1. Map of Lake Tanganyika and its position in East Africa. White circles with black outlines indicate locations of in situ temperature measurement. The size of the circle is proportional to the number of temperature measurements taken at each location. Most of the in situ data come from areas near major research centers (Uvira, Kigoma, and Mpulungu). The orange circle indicates the location of the TEX₈₆ sediment core and the red square indicates the location of the satellite data extraction site. The north, central, and south basins are located between 3.4-5.8 °S, 5.8-7.0 °S, and 7.0-8.9 °S, respectively.

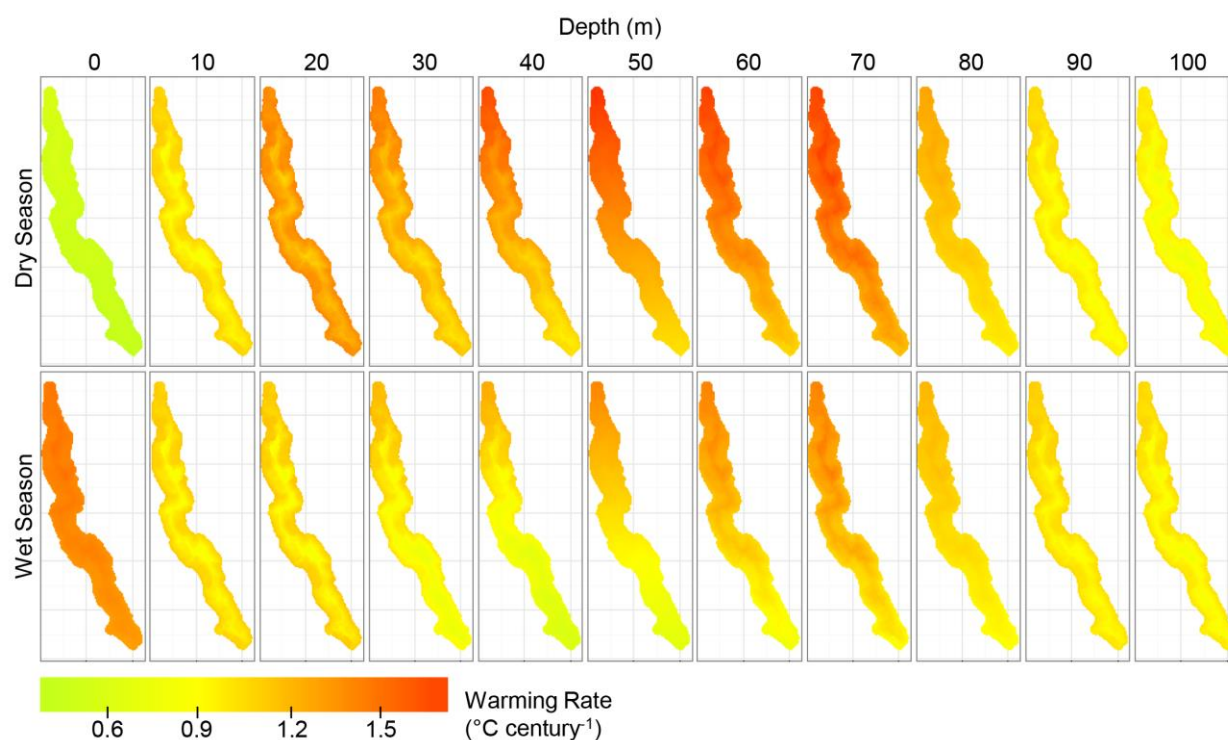


Fig. 2. Modeled century-long warming rate estimates (1912-2013). Each colored pixel on the maps is an estimate of the warming rate for that location in the lake based on the temperature model fit to all available in situ temperature data. Separate map panels show variation across seasons and depths in the estimated warming rate. The top row of warming estimate maps are for the dry season and the bottom row of warming rates are for the wet season. The columns indicate

the depth gradient of warming rate estimates from 0-100 m. All temperature models were fit to data from more than 1.5 km from land and in locations where the water depth exceeded 100 m deep.

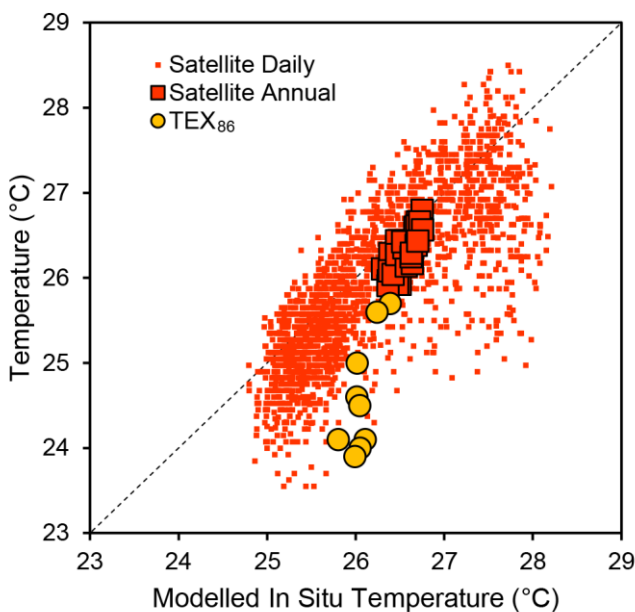


Fig. 3. Satellite temperature and TEX_{86} temperature as a function of modeled in situ temperature.

The black dashed line represents the 1:1 reference line. Small red square dots represent daily satellite temperatures as a function of the modeled in situ estimate at the satellite extraction site.

Large red square dots with black outlines represent annual mean satellite temperatures as a function of modeled annual mean in situ temperatures at the extraction site. Annual mean satellite temperatures were calculated from raw satellite data linearly interpolated to daily timescales.

Large orange circular dots with black outlines represent the TEX_{86} measurements as a function of the modelled annual mean temperature at the core site.

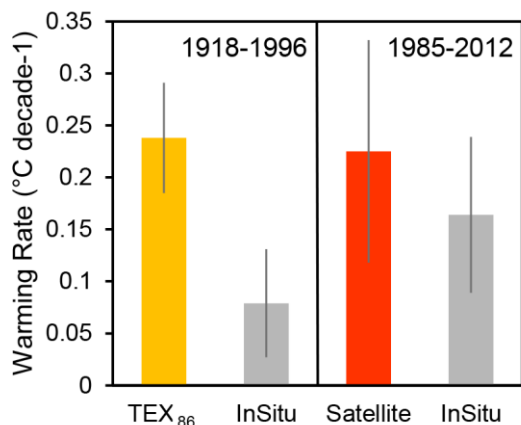


Fig. 4. Surface warming rates based on in situ, satellite, and TEX₈₆ data. Each bar represents a warming rate estimate based on one of the three temperature measurement methods (in situ, satellite, TEX₈₆). Error bars represent 95% confidence intervals for each estimate. The two leftmost bars are warming rate estimates over the period from 1918-1996 based on TEX₈₆ data and the in situ model output for the location and timeframe of the TEX₈₆ core. The two rightmost bars show warming rate estimates over the period from 1985-2011 based on satellites and in situ model output for the location and time frame of the satellite data extraction.

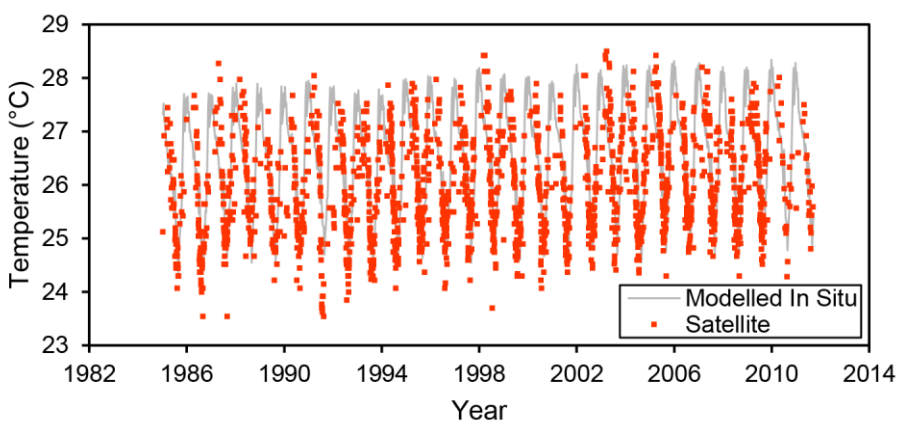


Fig. 5. Long-term satellite temperature data compared to model estimates. Each small red square dot is a raw, satellite measurement of the lake's surface. The grey line is the modeled surface

temperature at the location of the satellite extraction. Satellite temperatures closely track the seasonal, interannual, and long-term variation in temperature data predicted by in situ temperature data.

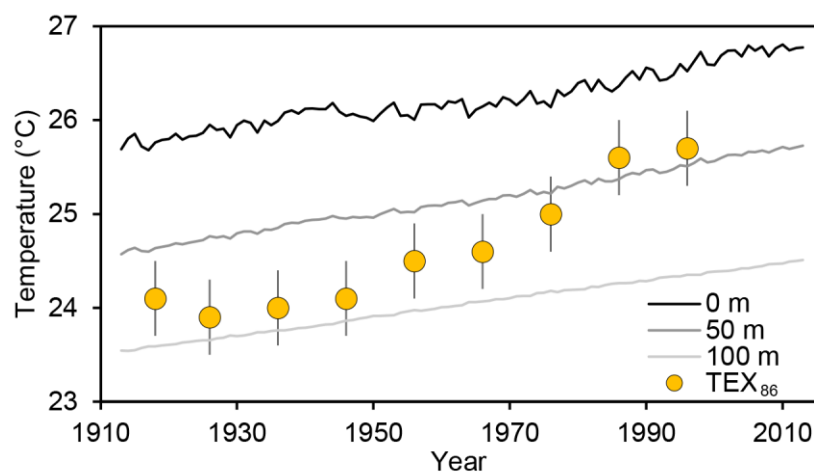
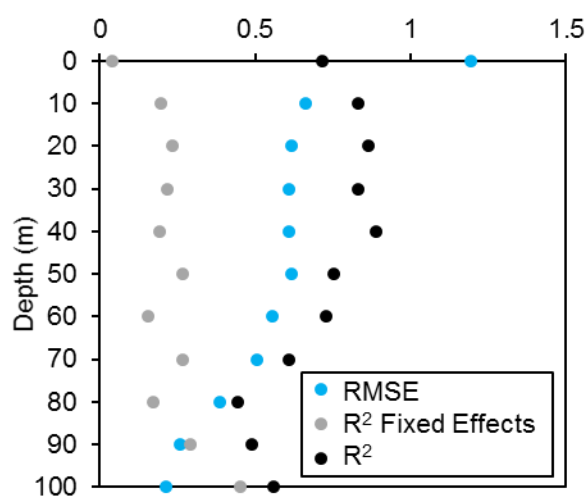


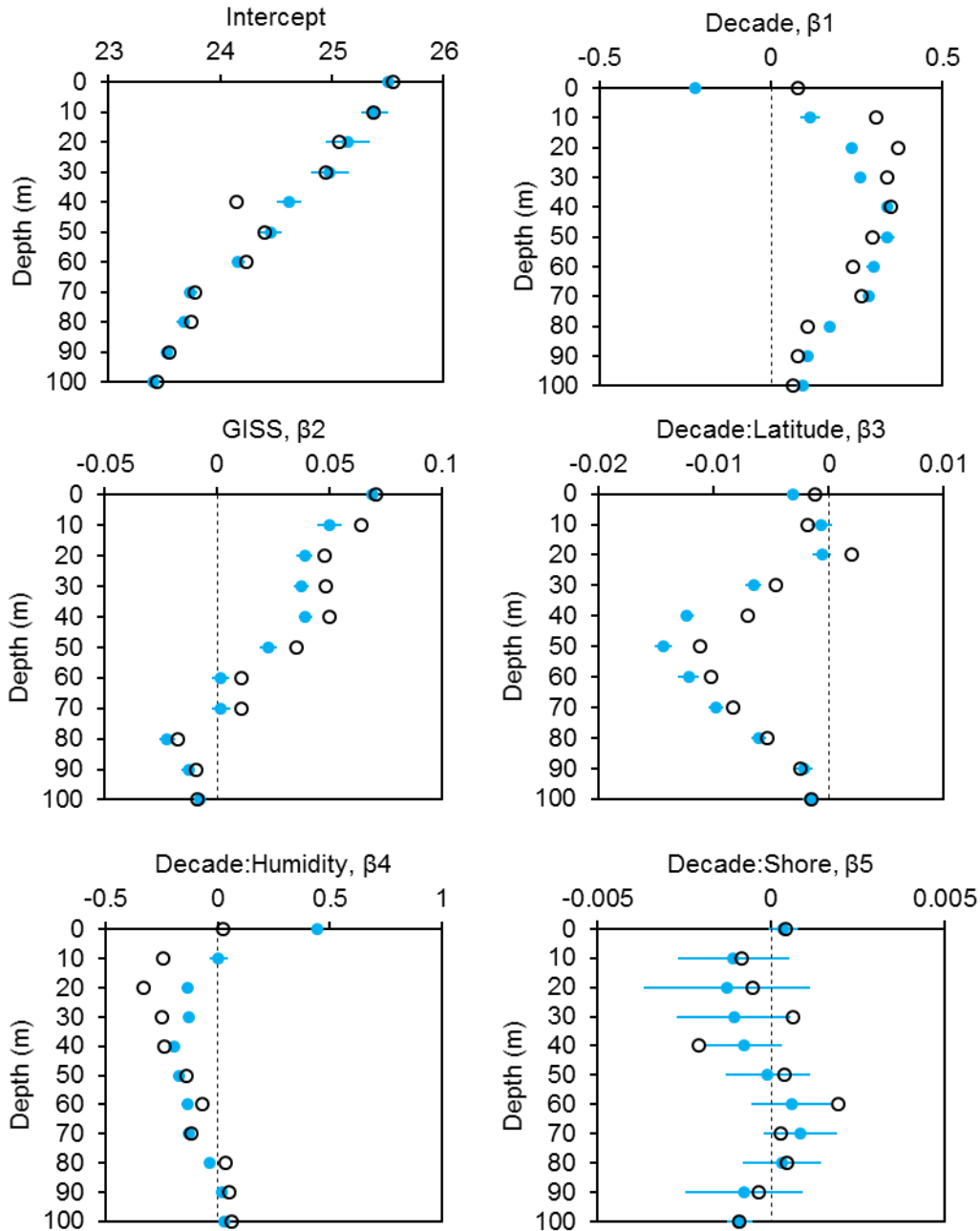
Fig. 6. Long-term TEX₈₆ temperature data compared to model estimates. Each large orange circular dot is a raw TEX₈₆ surface temperature measurement. Each TEX₈₆ measurement represents the annual mean surface temperature at the location of the TEX₈₆ core site $\pm 0.4^{\circ}\text{C}$ (95% confidence interval). The three lines are the modeled annual surface temperature at the location of the TEX₈₆ core site at three different depths (0, 50, 100 m). There is a strong disagreement between TEX₈₆ and modeled in situ temperatures, especially early in the time series. Deviations between the TEX₈₆ temperature measurements and the modeled surface temperature may reflect model error, error in the TEX₈₆ calibration procedure, or long-term shifts in the depth range of Thaumarchaeota (the microbes whose biomolecules are involved with generating the TEX₈₆ proxy).

Appendixes

Appendix 1. The vast majority of data in this compilation have not been included in previous long-term temperature trend estimation. In total, temperature data are now available from the years 1912-3 (Stappers 1913, Jacobs 1914), 1938-9 (Beauchamp 1939), 1946-7 (van Meel, Ludovic, Kufferath 1987), 1953 (van Meel, Ludovic, Kufferath 1987), 1955-7 (Dubois 1958), 1960-2 (Coulter 1968), 1964-6 (Coulter 1968), 1973 (Craig 1974), 1975 (Edmond et al. 1993), 1981-2 (Narita et al. 1986), and intermittently from 1991 through 2013 (Huttula 1997, Plisnier et al. 1999, Plisnier 2001, Verburg et al. 2003, O'Reilly et al. 2003, Corman et al. 2010, Durisch-Kaiser et al. 2011). A portion of the data from some of these sources has been used in previous analyses, but our inclusion of all three basins and both wet and dry seasons enabled us to use additional temperature data that was excluded from previous syntheses (Stappers 1913, Jacobs 1914, Beauchamp 1939, Coulter 1968, van Meel, Ludovic, Kufferath 1987). We also included data in our analyses from published sources that have never before been used in long-term temperature syntheses (Narita et al. 1986, Corman et al. 2010, Durisch-Kaiser et al. 2011). When raw data were not directly available, temperature data were digitized from figures in publications.



Appendix 2. Mixed effects model evaluation. Root mean squared error (RMSE) and coefficient of multiple determination (R^2) for mixed effects models fit to in situ temperature data as a function of depth. The variance explained by the fixed effects in each model is reported as “ R^2 Fixed Effects.”



Appendix 3. Fixed effects model parameters. The β terms in the figures are coefficients for the continuous, fixed effects in the in situ temperature models. These models characterize inter-annual and century-long variation in Lake Tanganyika temperature as a function of depth. β_1 , the coefficient for the *Decade* term, can be interpreted as the century-long warming rate for a specific depth ($^{\circ}\text{C decade}^{-1}$). β_2 , the coefficient for the *GISS* term, can be interpreted as the influence of global, inter-annual variation in temperature on upper water column temperatures in Lake Tanganyika. The β terms associated with the interaction terms in the model (β_3 , β_4 , and β_5) can be interpreted as the impact of latitude ($^{\circ}\text{S}$), relative humidity, and distance to shore (km) on the generalized warming rate estimate (β_1). Blue dots indicate the median coefficient estimate across all models fit to 10% subsets of temperature data. Error bars extending from the blue dots represent the standard deviation in model coefficient estimates across models fit to data subsets. The empty circles represent coefficients from the full models fit to all available temperature data at a specific depth.

Chapter 2: Morphometry and average temperature affect lake stratification responses to climate change*

Abstract

Climate change is affecting lake stratification with consequences for water quality and the benefits that lakes provide to society. Here we use long-term temperature data (1970-2010) from 26 lakes around the world to show that climate change has altered lake stratification globally and that the magnitudes of lake stratification changes are primarily controlled by lake morphometry (mean depth, surface area, and volume) and mean lake temperature. Deep lakes and lakes with high average temperatures have experienced the largest changes in lake stratification even though their surface temperatures tend to be warming more slowly. These results confirm that the nonlinear relationship between water density and water temperature, and the strong dependence of lake stratification on lake morphometry makes lake temperature trends relatively poor predictors of lake stratification trends.

Introduction

Lake stratification responses to climate change affect people around the world through their impacts on water quality. Intensified thermal stratification of lakes can exacerbate lake anoxia (Chapman et al. 1998, Hecky et al. 2010, Van Bocxlaer et al. 2012, Palmer et al. 2014, North et al. 2014), enhance the growth of planktonic, bloom-forming cyanobacteria (Steinberg and Hartmann 1988, Paerl and Huisman 2009, Paerl and Paul 2012), and changes to internal

* Published as Kraemer, B. M., O. Anneville, S. Chandra, M. Dix, E. Kuusisto, D. M. Livingstone, A. Rimmer, S. G. Schladow, E. Silow, L. M. Sitoki, R. Tamatamah, Y. Vadeboncoeur, and P. B. McIntyre. 2015. Morphometry and average temperature affect lake stratification responses to climate change. *Geophysical Research Letters*.

nutrient loading with consequences for lake productivity (Verburg et al. 2003, O'Reilly et al. 2003, Verburg and Hecky 2009). Despite the recognition that climate change effects on lake stratification are ubiquitous (Livingstone 2003, Coats et al. 2006, Saulnier-Talbot et al. 2014), global patterns in the impact of climate change on lake ecosystems including lake stratification remain uncertain (Adrian et al. 2009, Williamson et al. 2009).

Climate change has strongly influenced surface temperatures of lakes worldwide (Schneider and Hook 2010). The ecosystem consequences of climate change are often assumed to parallel warming rates (Smol et al. 2005, Solomon et al. 2007), but this is unlikely to be true of climate change effects on lake stratification. Due to the nonlinear relationship between water temperature and water density, the impact of temperature changes on lake stratification is highly dependent on average lake temperatures (Lewis 1987). Furthermore, lake stratification depends strongly on basin morphometric characteristics (mean depth, surface area, volume) (Lerman et al. 1995, Butcher et al. 2015) which may constrain lake stratification responses to warming. For instance, the capacity for lake warming to lead to thermocline depth shifts may be dampened in large lakes where the depth of the thermocline is strongly constrained by a lake's fetch (Gorham and Boyce 1989, Mazumder and Taylor 1994, Fee et al. 1996, Bohrer and Schultze 2008, MacIntyre and Melack 2010). Thus, predicting lake stratification responses to climate change may depend on understanding how patterns in warming rates intersect with a lake's baseline temperature and morphometry to alter its stratification regime.

Given the importance of lake stratification for lake biota and water quality, we aim to determine which of the 26 lakes in our analysis are most susceptible to stratification changes in response to climate change. We compiled temperature profile data from lakes on five continents to test whether mean lake temperatures, lake warming rates, or lake morphometry can be used to

predict the observed trends in lake stratification as indicated by the depth of the thermocline, the thermal stability of the water column (Schmidt stability), and the steepness of the thermocline (thermocline buoyancy frequency). Due to the extraordinary size and depth of some of the lakes in our analyses, they represent 3.0% of the cumulative lake surface area, and 44% of the cumulative liquid surface freshwater on earth. The broad range of lake locations and characteristics represented in our analyses (Appendix 2, Appendix 3) provides insights into controls on lake stratification trends and informs predictions of how the global population of lakes will respond to climate change.

Methods

Study Sites

We compiled temperature profiles for 26 lakes over the period from 1970-2010 from arctic, boreal, temperate, subtropical, and tropical regions. Temperature variation in these lakes have already been linked to climate change (Ambrosetti and Barbanti 1999, Quayle et al. 2002, Livingstone 2003, Lorke et al. 2004, Dokulil et al. 2006, Coats et al. 2006, Hampton et al. 2008, Moore et al. 2009, Schneider and Hook 2010, Hecky et al. 2010, Rimmer et al. 2011, Hsieh et al. 2011, Shimoda et al. 2011, Winslow et al. 2014) but several of the temperature time series in our study have not been previously published in their full length (Atitlan, Moss, Sombre, Heywood, Nkugute). The lakes included in our analysis represent a wide range of surface area (0.02 to 68800 km²), maximum depth (2.3 to 1642 m), and elevation (-212 to 1987 m above sea level) (Supplementary Table 1). All are freshwater lakes except for Lake Kivu which has a marked salinity gradient that affects its stratification. We analyzed the three basins of Lake Tanganyika independently as they span a significant latitudinal gradient, are separated by relatively shallow sills, and have divergent temperature and stratification trends. The temperature data for 5 lakes in

our analysis did not span the entire range from 1970-2010 but all lakes had temperature data which started in 1976 or earlier and ended in 2004 or later. Some lakes had only one profile per year while others had daily profiles from high resolution data loggers. Several lakes had data gaps of more than one year. The mean data gaps (average time between temperature profile measurements) for Tanganyika, Kivu, Victoria, Nkugute, and Atitlan were 2, 3, 3, 7, and 10 years, respectively. Sensitivity analyses showed that data gaps of this size do not significantly bias our stratification trend estimates (Supplementary Figure 1). The number of depths in each temperature profile varied across lakes from 8 to 16 depending on lake depth. We verified that the values for stability, thermocline depth, and thermocline strength that were calculated from temperature profiles with discrete depths closely matched those calculated based on high resolution temperature profiles when they were available.

Temperature and Stratification Trend Estimation

The mean surface temperature, whole-lake temperature (volume-weighted), and bottom temperature were calculated from each temperature profile. From these profiles, we also calculated the Schmidt stability (kJ m^{-2}), thermocline depth (m), and Brunt-Väisälä buoyancy frequency (s^{-1}) at the thermocline using LakeAnalyzer (Read et al. 2011). LakeAnalyzer used well-accepted methods of calculating lake stratification indices from in situ temperature profiles and hypsographic data. Schmidt stability (hereafter “stability”) is the amount of energy required per unit area to mix a lake to homothermy without the exchange of heat (Schmidt 1928, Idso 1973). Stability is a valuable metric because it is related to the potential for accumulation and depletion of deep water solutes in lakes (Kling 1988). The thermocline depth is the depth of the maximum density gradient in the water column and is a key variable controlling the depth niches of aquatic organisms (Weyhenmeyer et al. 2011). The Brunt-Väisälä buoyancy frequency

(hereafter “buoyancy frequency”) is the angular frequency at which a parcel of water would oscillate if it was displaced from its location in the water column. We calculated the buoyancy frequency at the thermocline for each temperature profile to estimate the steepness of the thermocline—a key control on vertical mixing in aquatic systems (Wüest and Lorke 2010). High buoyancy frequency signifies that the thermocline is steep and the resistance to vertical mixing at the thermocline is pronounced.

Changes in the timing of stratification were not analyzed here as several lakes were stratified year-round. However, we did determine the typical start and end date of stratification in lakes that mix completely; only temperature profiles taken during the stratified period were used for trend estimation. We estimated the typical start and end date of stratification by calculating the average day of the year (DOY) over the entire observation period (1970-2010) on which the density stratification was sufficient to develop a persistent (lasting more than 5 days), mid-water thermocline. Year-round data were used for lakes that are permanently stratified or partially stratified all year round.

To estimate trends in temperature and stratification indices during the stratified period, we removed the seasonal pattern from the temperature and stratification data and used Theil-Sen non-parametric regression for trend estimation (Theil 1950, Sen 1968). We removed the seasonal pattern by first calculating a 30-day running mean over the course of a seasonal data curve made up of data pooled from all years for each lake. Then, we calculated the difference between the 30-day running mean centered on each day of the year and the grand mean over the entire 40-year record. That difference was subtracted from raw measurements made on the same day of the year to remove variation in the data attributable to time of year when the measurement was made. The seasonal detrending procedure was carried out independently for surface

temperatures, whole-lake temperatures, bottom temperatures, and the three stratification indices. The non-parametric Mann-Kendall test was used to assess the significance of trends ($\alpha = 0.05$).

Predictors of stratification trends

Multiple linear regression models, hierarchical variance partitioning, and AIC model selection were used to determine the best predictors of trends in lake stratification indices. One value (the trend over time) was calculated for each lake stratification index for each lake. The trends were then used as response variables in the models. We used multiple linear regression models designed to predict the magnitude of the stratification trends from nine variables that fell into one of three categories: lake morphometric predictors (average depth, surface area, and volume), average temperature predictors (surface temperature, whole-lake temperature, and the difference between surface and bottom temperature) and temperature trend predictors (surface trend, whole-lake trend, and the difference between surface and bottom trends). Each lake was treated as a single observation of change through time. The response variables in each model (stability, thermocline depth, and buoyancy frequency trends) and the morphometric predictors were log transformed to attain normality in distributions, as confirmed by the Kolmogorov-Smirnov test. Published values were used for lake morphometric characteristics (maximum depth, mean depth, surface area, and volume).

We used Akaike's information criterion (AIC) (Akaike 1981, R Development Core Team 2013) forward and backward stepwise predictor selection to identify models that maximize explanatory power while minimizing the number of predictors (AIC selection criteria: $\delta AIC > 2$). The models for predicting stratification trends were refit using only the variables selected by the AIC. Using the most parsimonious model for trends in each stratification index, the significance of each predictor was assessed using the 95% confidence interval for its regression coefficient.

We also used hierarchical variance partitioning (Mac Nally 1996, R Development Core Team 2013) on each full model with all nine predictor variables to determine the independent contribution of each predictor variable to the total variance explained by the full multiple linear regression model. We compared across predictor variables and across categories of predictor variables (morphometric, average temperature, and temperature trends) to determine which variables had the most influence on the magnitude of stratification trends.

Results

Temperature and Stratification Trends

On average, lake surface temperatures, whole-lake temperatures, and bottom temperatures have warmed by 0.84°C, 0.43°C, and 0.05°C, respectively, over the period from 1970-2010 across the 26 lakes (Fig 1a). Significant increases in surface, whole-lake, and bottom temperature were observed in 20, 14, and 9 lakes, respectively (Mann-Kendall $p < 0.05$). Significant decreases were only observed in the bottom temperatures of one lake (Lake Pielinen, Mann-Kendall $p < 0.05$). Lake surface temperature trends, whole-lake temperature trends, and bottom temperature trends were positively related to latitude (Pearson's correlation coefficient, $r = 0.26, 0.18, \text{ and } 0.14$, respectively) and negatively related to mean depth (Pearson's correlation coefficient, $r = -0.22, -0.36, \text{ and } -0.21$, respectively).

Lake stratification is becoming more stable, with deeper and steeper thermoclines (Fig 1b). Of the 26 lakes, significant increases in buoyancy frequency, stability, and thermocline depth were observed in 17, 12 and 9 lakes, respectively (Mann-Kendall, $p < 0.05$). Only one lake had a significant decrease in buoyancy frequency (Mann-Kendall, $p < 0.05$) and no lakes had a significant decrease in Schmidt stability or thermocline depth (Mann-Kendall significance test, $p > 0.05$).

Predictors of stratification trends

Lake morphometric variables and the mean lake temperature are better predictors of lake stratification trends than lake warming rates. The morphometric predictors and average temperature predictors together explained a high percentage of the variance in stratification trends, while warming rates were comparatively unimportant. In sum, morphological variables and average temperature variables explained 94% of the explain variation in Schmidt stability trends, 81% of the explained variation in buoyancy frequency trends, and 83% of the explained variation in thermocline depth trends (Fig 2). Morphological variables were the best predictors of stability trends (70% of explained variance) and buoyancy frequency trends (64% of explained variance), while average temperatures were the best predictors of trends in thermocline depth (49% of explained variance). Mean depth explained the most variation in stratification trends across all three models (27%, on average, Fig 2, 3a). Lakes with greater mean depths had larger changes in their stability but slightly smaller changes in buoyancy frequency (Fig 3a). Of the average temperature predictors, average surface temperature explained the most variation in stratification trends (12%, Fig 2, 3b). Lakes with higher surface temperatures had larger changes in stability and thermocline depth but small buoyancy frequency trends (3b). Temperature trends explained little of the variation in stability (4%), thermocline depth (4%), and buoyancy frequency (6%) trends, respectively. Thus, multiple linear regression models of stratification index trends are largely unaffected by removing warming rates from the model (Fig. 4).

According to AIC, the best predictors of stability trends were mean depth, average whole-lake temperature, and the average difference between surface and bottom temperature. All three variables were significant predictors of stability trends (multiple linear regression, $R^2 = 0.91$, $p < 0.05$). The best predictors of thermocline depth trends were lake volume, average

whole-lake temperature, and average difference between surface temperature and bottom temperature. All three were significant predictors but the resulting model explained considerably less of the variation in thermocline depth trends (multiple linear regression, $R^2 = 0.60$, $p < 0.05$). The best predictors of buoyancy frequency were mean depth, volume, and whole-lake warming rate. Mean depth and volume were significant predictors of trends in buoyancy frequency (multiple linear regression, $p < 0.05$) while whole-lake warming rate was not (multiple linear regression, $p = 0.11$). The resulting model explained a relatively small proportion of the variance ($R^2 = 0.40$, $p < 0.05$). Moderate non-random patterning in the residuals of models for thermocline depth and buoyancy frequency suggested that the models overestimated trends when the observed change was small and underestimate trends when the observed change was large.

Discussion

Lake stratification in the 26 lakes in our analysis has become more stable with deeper and steeper thermoclines. The consistency of the trends across lakes suggests a global driver of these changes over the last 40 years. Of the predictor variables that we investigated, lake morphometric variables and mean lake temperature explain the most variation in the magnitude of stratification trends across lakes. Knowing a lake's surface temperature trend, its whole-lake temperature trend, and the difference between its surface and bottom temperature trend does not considerably increase our ability to predict its stratification responses to climate change.

Changes in lake stability increase as a function of lake depth, as has been shown previously at the regional scale (Butcher et al. 2015). This finding suggests that the extension of the stratified season in lakes that fully mix or the reduction in the spatial extent of mixing in lakes that partially mix will be most common in deep lakes. In contrast to lake stability, the magnitude of shifts in buoyancy frequency were negatively correlated to lake depth. Thus, higher

turbulent energy in large lakes (Gorham and Boyce 1989) may make the depth of the thermocline more resistant to change even as the surface warms. Thus, global patterns in the responses of lake stability to climate change will, in part, depend on global patterns of lake depth. Regions with many large, deep lakes may be most susceptible to ecosystem changes associated with increases in lake stability, while regions with many small lakes may be most susceptible to ecosystem changes associated with the strength of the thermocline.

Stability and thermocline depth trends were positively related to lake surface temperature with warmer lakes having larger changes in stability and thermocline depth. This suggests that lake stratification patterns may be more sensitive to climate change in the tropics than in temperate and arctic regions because lake temperature during the stratified period in each lake was strongly correlated to lake latitude. This observed pattern echoes previous work which used numerical simulations to show that lake stratification in warm, tropical lakes is more sensitive to changing surface temperatures (Lewis 1987). This latitudinal gradient in lake stratification sensitivity arises from the nonlinear relationship between water temperature and water density. The magnitude of thermocline shifts was also dampened in lakes with large temperature differences between the surface and bottom temperatures. Surface-bottom temperature differences tend to be greatest at mid-latitudes, thus reducing thermocline shifts there.

Long-term temperature monitoring is carried out in only a small fraction of the world's lakes which limits the predictive capacity of our statistical models. For instance, climate change-mediated shifts in water clarity (Gaiser et al. 2009), lake level (Coops et al. 2003), and wind speed [Young et al., 2011] may explain a large portion of the variation left unexplained by our lake stratification models. Our predictions of global lake stratification responses to climate change could be improved considerably by accounting for regional and lake-specific changes in

these variables. Future work with more lakes will be less encumbered by the risk of model overfitting and will be free to incorporate these variables as predictors.

We urge caution in the use of our models to predict lake stratification responses to climate change for certain lake types that are not well-represented in our analyses. While the lakes in our analyses represent 44% of the global liquid surface freshwater, they represent only 2.2×10^{-5} % of all lakes on earth (Verpoorter et al 2014). The lakes with the most consistent, data-rich, in situ temperature profile records are almost all from temperate, subarctic, and arctic regions; relatively few are from tropical and subtropical regions. Of the tropical lakes included in our analyses, rift lakes and crater lakes are overrepresented. In reality, most tropical lakes may be fluvial in origin (Lewis 1987), but to our knowledge there are no fluvial lakes with long-term temperature profile datasets. Most long-term lake temperature monitoring programs initiated during the last few decades still focus on mid and high-latitude lakes, so this bias is unlikely to be remedied in the near future (but see (Saulnier-Talbot et al. 2014)). Remote sensing has circumvented this bias for surface temperatures, but our results show that surface temperature trends have little association with shifts in stratification. Unfortunately, understanding lake stratification requires temperature profile data, which are challenging to collect on a regular basis. Given the significant increases in stratification observed in most of the lakes analyzed in this study, it is clear that understanding the effects of climate change on the world's lakes will require a much broader monitoring network for temperature profiles.

While we did not include ecological data in our analyses, the stratification trends analyzed here have direct implications for lake ecosystem dynamics. The shifts in lake stratification will intensify the confinement of dissolved oxygen, nutrients, particles, and non-motile organisms to specific lake strata with profound effects on lake ecosystems (O'Reilly et al.

2003, Adrian et al. 2009, Shimoda et al. 2011, North et al. 2014). Our results indicate that while stratification changes are likely to be felt across latitude, deep tropical lakes like the African rift lakes, the ancient lakes of Indonesia, and the crater lakes of Central America may be most susceptible to shifts in lake stratification. The resulting ecological shifts that may result are particularly hazardous because tropical lakes provide critical sources of nutrition to adjacent human populations and tend to be hotspots of freshwater biodiversity (Vadeboncoeur et al. 2011, Brawand et al. 2014).

Conclusion

In situ temperature profile observations from 26 globally distributed lakes were used to study how lake warming rates intersect with a lake's baseline temperature and morphometry to alter its stratification. Calculations of lake mixing indices over time from 1970-2010 showed that on average, lake stratification is becoming more stable with deeper and steeper thermoclines. The magnitude of stratification responses to climate change across lakes were associated with lake average temperature and morphometry, but not with warming rates. These results suggest that the influence of climate change on lake temperature and stratification is ubiquitous, but may be felt most strongly in large tropical lakes.

Acknowledgements

We are grateful for field research funding from the National Science Foundation (NSF) (DEB-1030242), and encouragement from the Global Lake Temperature Collaboration (DEB-1147666, National Aeronautics and Space Administration (NASA), Research Opportunities in Space and Earth Sciences (ROSES) Grant, Institute of Agricultural and Natural Resources (IANR), University of Nebraska-Lincoln). Signy Island lake (lakes Heywood, Moss, Sombre) temperature

data was contributed by the Polar Data Centre under a British Open Government License, British Antarctic Survey, 1963-2004 (GB/NERC/BAS/AEDC/00063)

(http://www.antarctica.ac.uk/bas_research/data/access/index.php). Long-term monitoring of Lake Tanganyika temperature data was by Timo Huttula, Pekka Kotilainen, Catherine O'Reilly, Anu Peltonen, Pierre-Denis Plisnier, Jouku Sarvala, and Bernhard Wehrli and others. Lake Kivu data were supplied by Francois Darchambeau, Jean-Pierre Descy, Alberto Vieira Borges, and Martin Schmid and funded by the ARES-CCD through the "ECOSYKI : Studies on Lake Kivu ecosystem for its sustainable management" project, by the Belgian Federal Science Policy Office through the "EAGLES: East African Great Lake Ecosystem Sensitivity to Changes" (EAGLES, SD/AR/02A) project, and by the Fonds National de la Recherche Scientifique (Belgium) through the "CAKI: Cycle du Carbone et des Nutriments au Lac Kivu" and "MICKY: Microbial Diversity and Processes in Lake Kivu" projects (data contact: Jean-Pierre Descy, jpdescy@gmail.com) . Lake Tahoe temperature data collection has been funded by the Tahoe Regional planning Agency, Lahontan Regional Water Quality Board and contributed by the UC-Davis Tahoe Environmental Research Center (data available at <http://terc.ucdavis.edu/>). Lake Atitlan temperature data collection was funded by UVG and USAID (data contact: Margaret Dix, margeret.dix@gmail.com). Lake Baikal temperature data collection was partially funded by the Russian Ministry of Education and Science, (GR 01201461929) (data contact: Eugene Silow, eugenasilow@gmail.com). Data from Toolik Lake, Lake Mendota, and Trout Lake were provided by the National Science Foundation's Long-Term-Ecological Research program (data sets titled, North Temperate Lakes LTER: Physical Limnology of Primary Study Lakes, Physical and chemical data for various lakes near Toolik Research Station, Arctic LTER, <http://www.lternet.edu/lter-sites>). Lake Kinneret temperature data were accessed through the

Yigal Allon Kinneret Limnological Laboratory (data available through the Lake Kinneret Data Center, <http://www.ocean.org.il/Eng/KinneretDataCenter/ProfileDC.asp>). Data from Lake Zurich were provided by the City of Zurich Water Supply (WVZ). Data from Greifensee were provided by the Amt für Abfall, Wasser, Energie und Luft, Canton of Zurich. Data contact for lakes Zurich and Greifensee is David Livingstone, David.Livingstone@eawag.ch. Data from Lake Geneva were from SOERE OLA-IS, INRA Thonon-les-Bains, CIPEL, [downloaded on January 2014], developed by Eco-Informatics ORE INRA Team (data contact: Orlane Anneville, orlane.anneville@thonon.inra.fr). Lake Biwa data were shared by Akihiko Oyama (gf30@pref.shiga.lg.jp) of the Shiga Prefectural Fishery Experiment Station. Data for lakes Rawson, 227, and 302 were contributed by the Experimental Lakes Area of Fisheries and Oceans-Canada (data freely available after signing data use agreement at www.experimentallakesarea.ca). Data from Castle Lake were contributed by the Aquatic Ecosystems Analysis Laboratory, University of Nevada-Reno (data contact: Sudeep Chandra, limnosudeep@me.com). Lake Nkugute data are from “CLANIMAE” report: Science for Sustainable Development, 2010 (<http://www.belspo.be/belspo/ssd/science/Reports/CLANIMAE%20FinRep%20PH%201.pdf>). Summer mean annual surface temperatures from 1985-2009 are available for the lakes in this analysis at [doi:10.1038/sdata.2015.8](https://doi.org/10.1038/sdata.2015.8).

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Figures

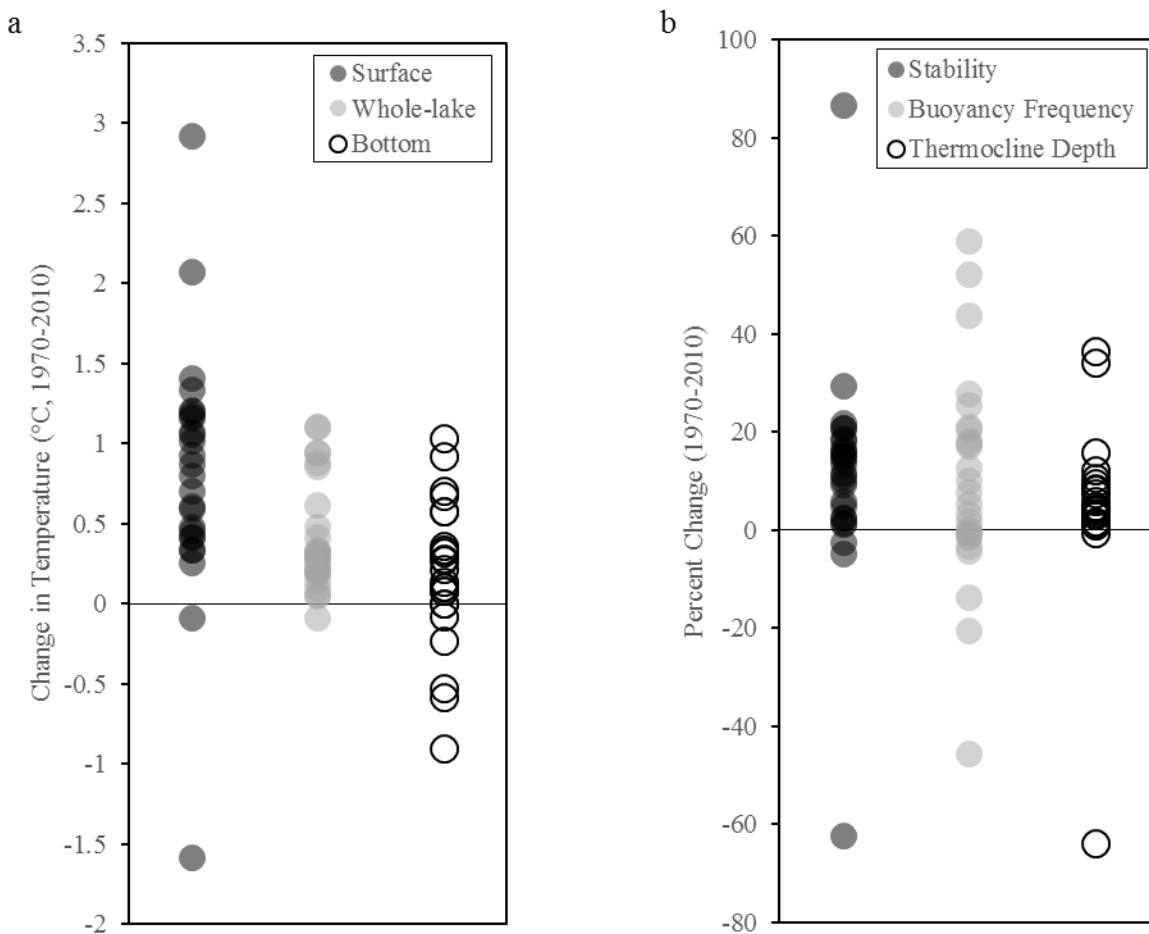


Fig 1. (a) Temperature change (Theil-Sen slope) for 26 globally distributed lakes (1970-2010).

(b) The associated percent change in three lake stratification indices (1970-2010).

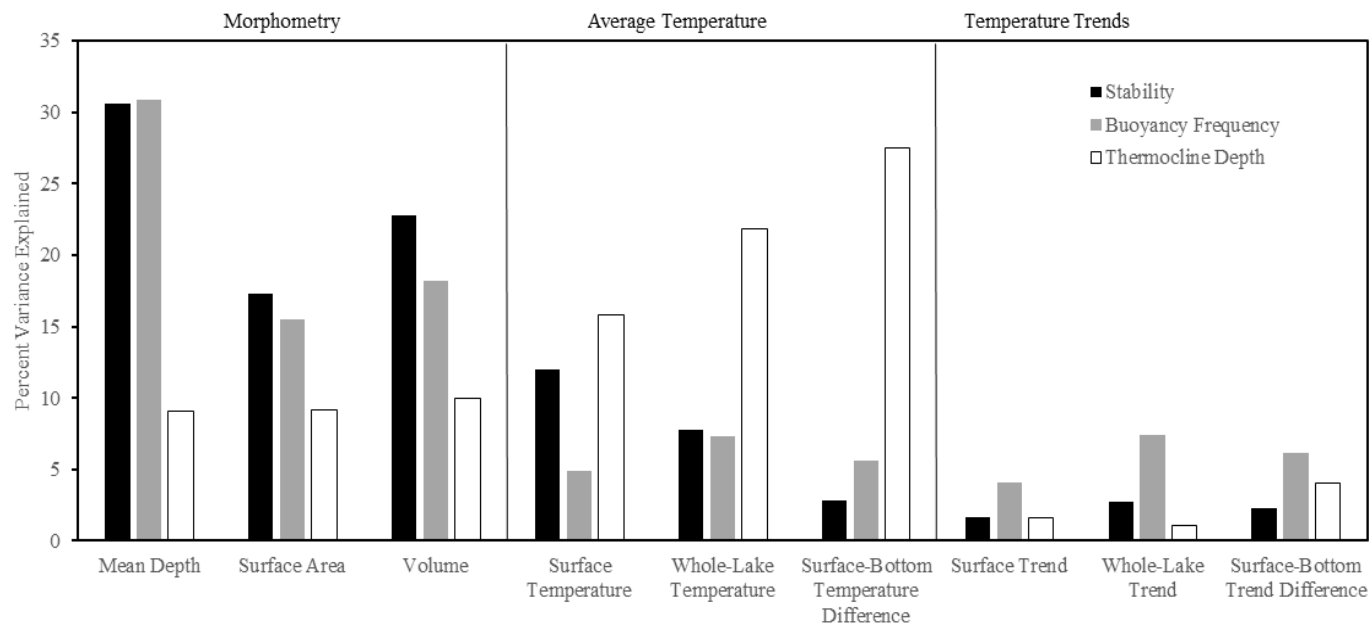
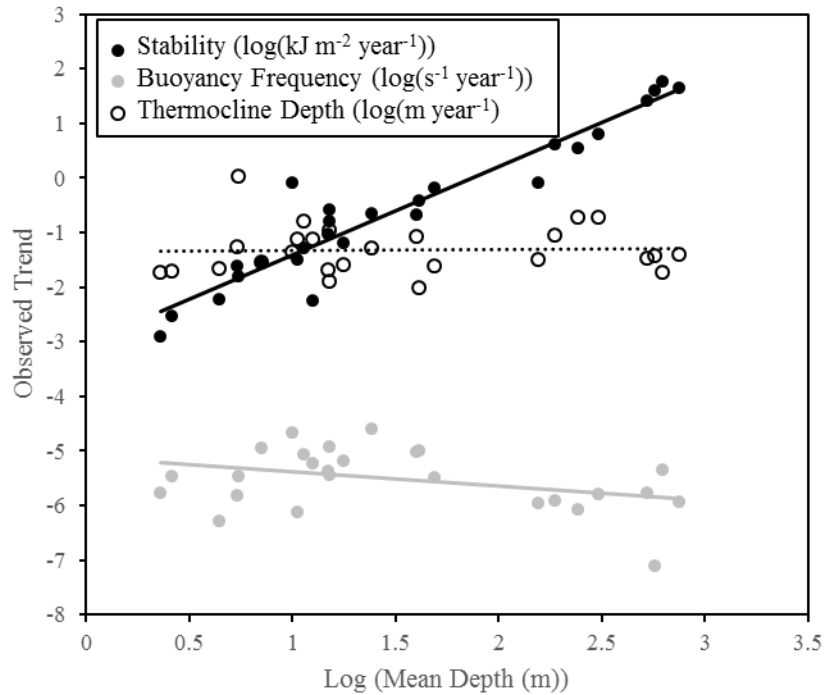


Fig 2. The variance in long-term (1970-2010) trends in lake stratification indices explained by 9 predictor variables as a percentage of variance explained by the full model. Predictor variables for each stratification index are grouped by morphometry, baseline temperature, and warming rate. All bars of a given shade sum to 100%.

a



b

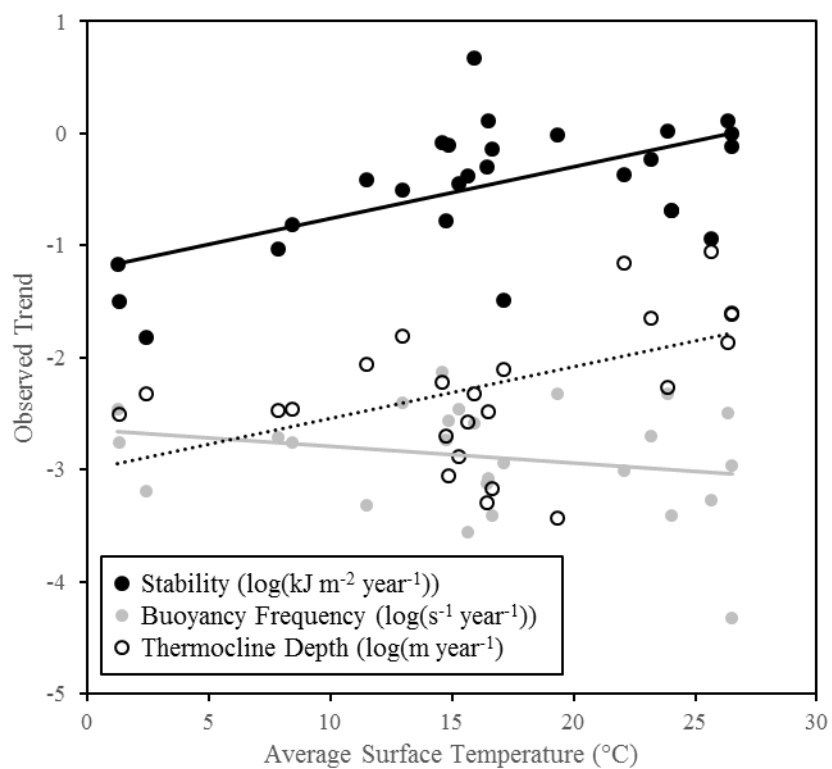


Fig 3. (a) Long-term (1970-2010) trends in lake stratification indices as a function of mean depth. Variance in trends explained by baseline temperature has been removed. (b) Long-term (1970-2010) trends in lake stratification indices as a function of the average surface temperature across the entire time series. Variance in trends explained by lake morphometry has been removed.

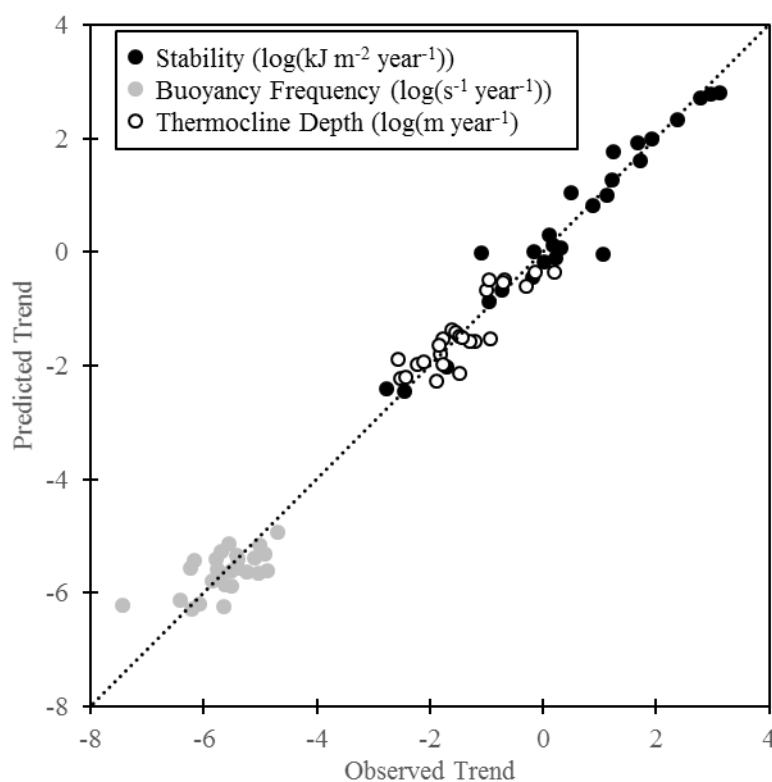
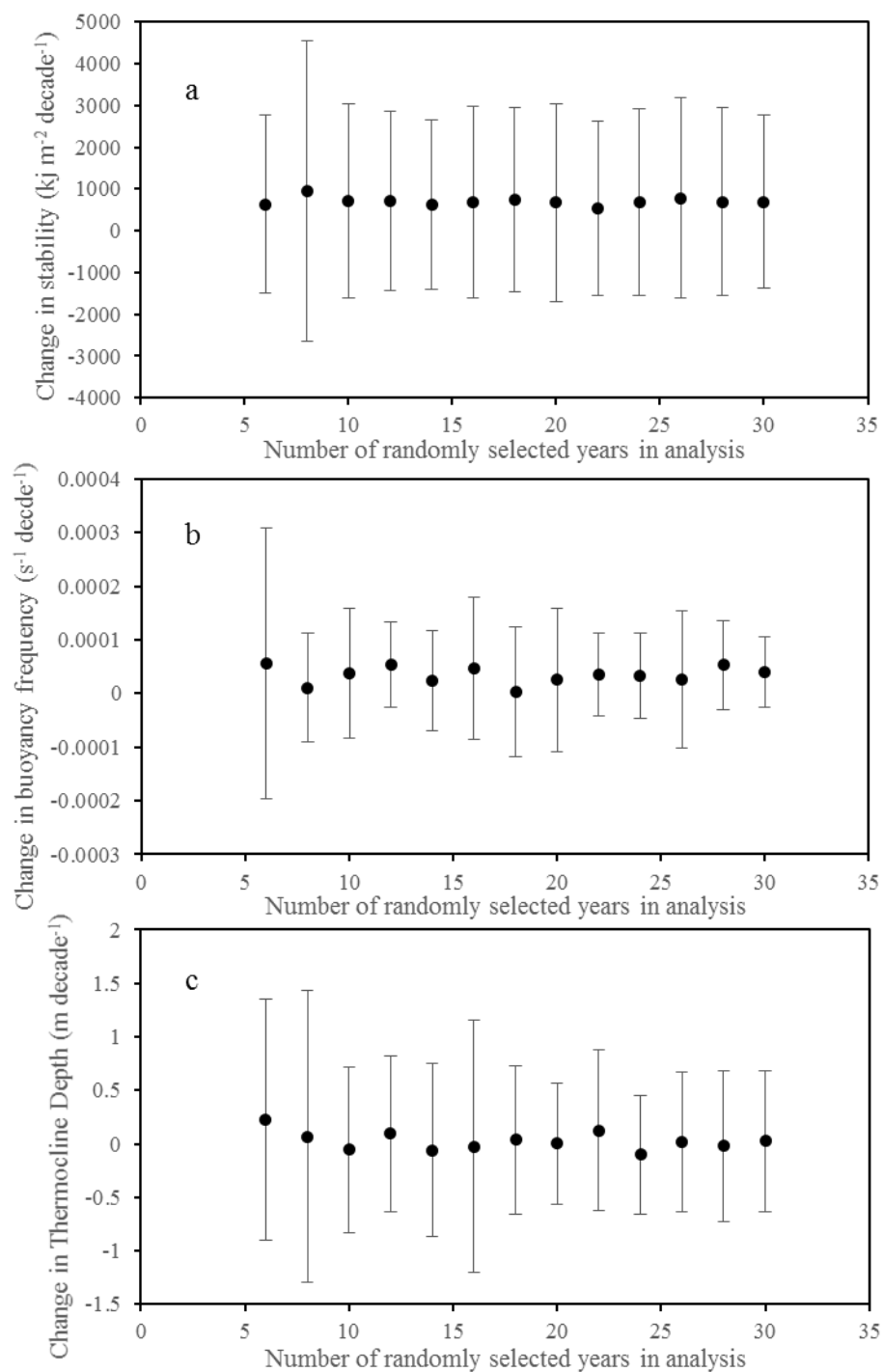


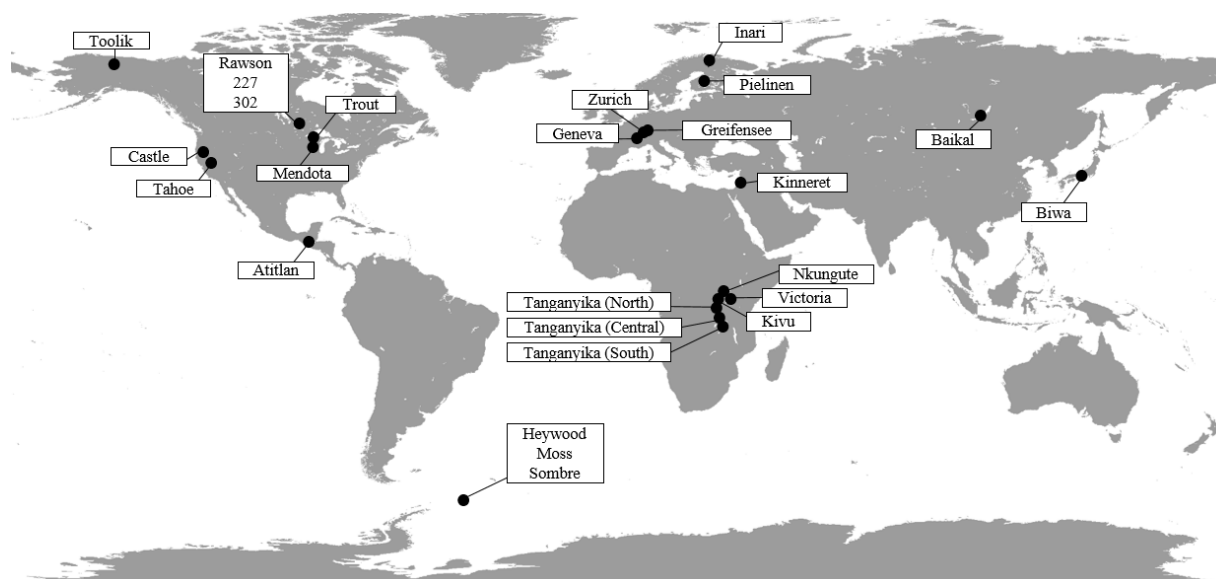
Fig 4. Predicted stratification trends versus observed stratification trends. Statistical models were fit to lake stratification data and used to predict the magnitude of long-term (1970-2010) stratification trends in each lake. Predicted trends here use models without warming rates as predictors. Predictors in the model included morphometric variables (mean depth, surface area, and volume) and average lake temperature variables (surface temperature, whole-lake temperature, and the difference between surface and bottom temperature). We compare predicted

trends from statistical model output to the actual long-term trend based on in situ temperature data from each lake.

Appendix



Appendix 1. We performed sensitivity analyses to determine whether our estimation of long-term trends in lake stratification indexes was sensitive to the number of years of temperature profiles used in trend estimation. Our first approach to this sensitivity analysis was to select the 19 lakes which had data for at least 30 years between 1970 and 2010. We then plotted the average long-term (1970-2010) trend in lake stratification indexes for all lakes as a function of progressively greater numbers of randomly selected years of data from 6 to 30. The average stratification trend across those 19 lakes was found to be insensitive to the number of years of data included in trend estimation. We also fit the models described in the first paragraph of section 3.2 with “data years” and “data depths” as predictors in the model. In all cases, “data years” and “data depths” were not significant predictors of long-term stratification trends (multiple linear regression $p > 0.05$). This suggests that the richness of data from each lake did not bias our long-term trend estimates. The algorithms used by LakeAnalyzer are ideal when stratification indices are being calculated from discrete depth temperature profiles. We also verified that the values for stability, thermocline depth, and thermocline strength calculated with LakeAnalyzer from temperature profiles with discrete depths closely matched those calculated based on high-resolution temperature profiles. Much of the temperature data included in our analysis is published in the DataONE and LTER data repositories. Metadata for these datasets contain more information about the temperature measurements included in our analyses.



Appendix 2. Map of study locations.

Lake characteristics

Lake	Max depth (m)	Mean depth (m)	Surface area (km ²)	Latitude (S/N)	Elevation (m)	Type	Continent	Data years	Data depths
Heywood	6	2.3	0.04	-60.68	4	Subantarctic	Antarctica	29	13
Moss	11	2.6	0.02	-60.72	48	Subantarctic	Antarctica	24	18
Sombre	12	5.5	0.02	-60.72	10	Subantarctic	Antarctica	30	14
TanganyikaS	1470	623	10617.83	-7.75	773	Tropical	Africa	10	16
TanganyikaC	885	521	9066.33	-6.26	773	Tropical	Africa	8	16
TanganyikaN	1310	572	13215.84	-4.65	773	Tropical	Africa	21	16
Kivu	480	240	2700	-2.05	1460	Tropical	Africa	12	18
Victoria	83	40	68800	-0.76	1133	Tropical	Africa	14	17
Nkugute	58	15	0.79	-0.32	1080	Tropical	Africa	6	18
Atitlan	340	188	130.1	14.70	1562	Tropical	North America	6	18
Kinneret	47	24	166	32.83	-212	Subtropical	Asia	41	12
Biwa	104	41	670.4	35.33	86	Subtropical	Asia	38	12
Tahoe	501	305	495	39.10	1897	Temperate	North America	41	18
Castle	34	11.4	0.2	41.19	1657	Temperate	North America	41	18
Mendota	25	12.5	39.88	43.11	259	Temperate	North America	41	18

Trout	36	14.9	16.08	46.05	494	Temperate	North America	31	18
Geneva	310	154	580.03	46.43	372	Temperate	Europe	41	12
Zurich	136	49	66.6	47.22	406	Temperate	Europe	41	18
Greifensee	32	17.6	8.45	47.35	435	Temperate	Europe	41	14
227	10	4.4	0.05	49.68	370	Temperate	North America	41	15
302	14	5.4	0.24	49.67	370	Temperate	North America	34	15
Rawson	30	10.5	0.56	49.66	370	Temperate	North America	41	12
Baikal	1642	744	31722	53.51	456	Subarctic	Asia	40	14
Pielinen	60	9.9	894.21	63.25	94	Subarctic	Europe	31	17
Toolik	26	7.1	1.5	68.63	720	Arctic	North America	33	18
Inari	92	15	1040.28	69.03	119	Arctic	Europe	41	12

Appendix 3. Physical characteristics of 26 focal lakes. The “Data Years” column indicates the number of years with temperature data for each lake dispersed over the period from 1970-2010. The “Data Depths” column indicates the number of depths with raw temperature data across all years which span the depth range of each lake. Lake Tanganyika’s three basins are separated by relatively shallow sills and span a broad latitudinal gradient. Here, we analyzed the three basins independently due to variation across basins in baseline temperature, warming rates, and stratification index trends. Surface temperature data from all lakes came from the top 1 m of the water column. Bottom temperature data were taken from the deepest measurements in each profile with consistent measurements across years for each lake. Bottom temperature data were typically from within 1-10 meters of the deepest point of the lake and always in the isothermal zone below the thermocline.

Chapter 3: Activation energies affect global patterns of lake metabolic responses to climate warming*

Abstract

Ecosystems are sensitive to climate warming in part due to the direct temperature dependence of metabolism. The direct effect of climate warming on metabolism in a specific ecosystem will depend on the ecosystem's average temperature, its warming rate, and the sensitivity of the metabolic response to temperature often represented by its activation energy. Given that patterns in temperature, warming rates, and activation energies vary substantially across ecosystem types, a wide range of global patterns in metabolic responses to temperature change can emerge when ecosystems warm. Here we use observed, long-term variation in lake temperature from 271 globally distributed lakes along with 94 empirically-derived freshwater activation energies to estimate the magnitude and distribution of direct lake responses to warming from 1970-2010. Lake metabolic responses to warming tended to be greatest in warm lakes for the bulk of freshwater metabolic responses even when cold lakes were warming faster, suggesting that relatively few metabolic responses to warming will parallel warming rates. Metabolic responses with low activation energies were most likely to parallel warming rates, signifying that activation energies provide a simple heuristic for predicting variation among traits in the geographic patterns of responses to warming. The direct metabolic consequences of lake warming for freshwater ecosystems are likely to be most strongly felt in tropical freshwaters where human well-being and freshwater biodiversity may be most affected.

* Prepared for submission with co-authors Sudeep Chandra, Margaret Dix, Esko Kuusisto, David M. Livingstone, Geoffrey Schladow, Eugene Silow, Lewis M. Sitoki, Rashid Tamatamah, Peter B. McIntyre

Introduction

Many biochemical reactions respond nonlinearly to variation in temperature due to fundamental chemical kinetics. The relationship between temperature and biochemical reaction rates is described by the Boltzmann-Arrhenius factor,

$$v \propto e^{-E_a/kT}$$

where v is the reaction rate, e is Euler's number (2.718), E_a is the activation energy (eV), k is the Boltzmann constant (8.617×10^{-5} eV K⁻¹), and T is the temperature (°K). A key feature of this equation is that as the activation energy of a reaction rate (E_a) approaches kT , the steepness of the nonlinear relationship between temperature and reaction rate is dampened (i.e., approaches linearity with a fixed slope) (Fig 1). Thus, the sensitivity of a given chemical reaction rate to temperature is linked to its activation energy; a higher activation energy connotes higher sensitivity to temperature changes which arises from a steeper exponential response to temperature (Fig 1).

Nonlinear biochemical responses to temperature are manifest at the cellular, organismal, and ecosystem levels (Gillooly *et al.*, 2001; Dell *et al.*, 2011; Yvon-Durocher *et al.*, 2012, 2014). For instance, the temperature dependence of gross primary production in forests is thought to reflect the temperature dependence of RUBISCO carboxylation of CO₂—a key rate-limiting step in photosynthesis (Yvon-Durocher *et al.*, 2010). Organismal metabolic rates (Gillooly *et al.*, 2001), carbon cycling rates (Bond-Lamberty & Thomson, 2010; Yvon-Durocher *et al.*, 2012), and ecosystem greenhouse gas emissions (Gudasz *et al.*, 2010; Dell *et al.*, 2011; Marotta *et al.*, 2014; Yvon-Durocher *et al.*, 2014) all respond exponentially to temperature due to the fundamental temperature dependence of chemical reactions underlying these processes.

Estimates of metabolic responses to warming based on Boltzmann-Arrhenius equations suggest that the ecological consequences of warming can be uncorrelated to variation in warming rates (Dillon *et al.*, 2010; Marotta *et al.*, 2014). For instance, in regions where baseline temperatures are high, a small temperature increase can lead to larger absolute responses than in areas where baseline temperatures increase faster from a lower starting point (Dillon *et al.*, 2010; Marotta *et al.*, 2014). It is estimated that climate change has had larger absolute effects on the metabolic rates of terrestrial ectotherms in the tropics even though air temperatures are increasing faster at higher latitudes (Dillon *et al.*, 2010). But when the activation energy of a metabolic rate is low, the temperature dependence relationship approaches linearity and we expect the resulting patterns in responses to temperature change to parallel warming trends. Moreover, if sites with low initial temperatures are warming sufficiently fast, the resulting change in metabolic rates might still be greater than sites with higher initial temperatures despite nonlinear responses. Thus, a wide range of global patterns in ecosystem responses to temperature change could emerge when a given response is exponential. Understanding how temperature and warming patterns intersect with that ecosystem's temperature sensitivity in a particular ecosystem type is essential for developing heuristics that guide understanding of patterns in ecosystem responses to warming.

Here we use long-term lake temperature data and well-characterized exponential relationships between temperature and metabolic responses to explore how they intersect to produce variation among lake ecosystems in the effects of climate warming. Lakes tend to be warming faster (Schneider & Hook, 2010) and have lower activation energies than terrestrial or marine environments (Dell *et al.*, 2011), suggesting that ecosystem responses in lakes are much more likely to parallel warming rates. We test whether the direct influence of temperature on

metabolism will or will not parallel warming rates for the bulk of metabolic responses in lakes. Lakes are ideal ecosystems for quantifying the effects of warming because their global geographic distribution and mutual independence make them sensitive sentinels of climate change (Adrian *et al.*, 2009; Schindler, 2009). Moreover, changes in lake ecosystem traits are likely to affect key provisioning and cultural ecosystem services (Wilson & Carpenter, 1999; Bennett *et al.*, 2009; Allan *et al.*, 2015), global carbon cycling (Tranvik *et al.*, 2009), and freshwater biodiversity (Vadeboncoeur *et al.*, 2011).

Materials and Methods

We conducted parallel analyses on temperature data from two lake temperature datasets: one dataset that takes advantage of depth-specific temperature data, and another that includes temperature data from more lakes but with average summer surface temperature only. Together, these two temperature data sources offer complementary approaches that demonstrate the value of rich geographical coverage across the globe and rich depth coverage within lakes for estimating direct metabolic responses to warming. We analyzed time series of temperature from multiple depths at 26 lake monitoring sites to ascertain how metabolic rates in lakes are expected to respond to warming as a function of lake depth. The 26 lake monitoring sites had a global distribution, and represent a wide range of morphometric characteristics (mean depth, surface area, volume). To further capture global trends, we also analyzed time series of average, summer surface temperatures from 271 lakes from a published database (Sharma *et al.*, 2015), yielding greater geographic representation but with less temperature data per lake. 19 lakes had data from both data sources. We substitute lake temperature data from both sources into Boltzmann-Arrhenius equations relating temperature to 94 metabolic responses to estimate metabolic change through time.

Annual lake temperature data

We compiled temperature profiles encompassing the entire annual temperature cycle for the 26 lake monitoring sites where such data were available. These 26 lake monitoring sites represented a wide range of surface area (0.02 to 68800 km²), depth (2.3 to 1642 m), and elevation (-212 to 1987 m above sea level). The 26 lake monitoring sites had on average 30 years of temperature profile data (range: 6-41 years) over the period from 1970-2010. To estimate metabolic rates through time as a function of lake temperature, we substituted surface and bottom temperature data from each lake into general Boltzmann-Arrhenius equations for 94 organismal and ecosystem traits. The output from these calculations can be interpreted as daily estimates of metabolic rates in a given lake based on the direct effect of temperature alone at a specific depth.

The activation energies for these traits were derived empirically from a combination of field and laboratory data using Boltzmann-Arrhenius model fitting to raw data. Field and laboratory data were obtained from online published databases (Dell *et al.*, 2013) and extracted from peer-reviewed publications (Gillooly *et al.*, 2001, 2002; Yvon-Durocher *et al.*, 2012, 2014). We only included data that were measured at temperatures below the temperature where the maximum metabolic rate was observed. When more than one species or ecosystem type was represented in the data set for a given trait, the median activation energy for that trait was used in our study. All traits show nonlinear temperature dependence and represent a gradient of activation energies. The lake traits analyzed here included methane emissions (0.96 eV) (Yvon-Durocher *et al.*, 2014); invertebrate metabolism (0.74 eV) (Gillooly *et al.*, 2001), pelagic ecosystem respiration (0.63 eV) (Yvon-Durocher *et al.*, 2012), benthic ecosystem respiration (0.55 eV) (Yvon-Durocher *et al.*, 2012), fish metabolism (0.41) (Gillooly *et al.*, 2001), and

planktonic gross primary production (0.35) (Yvon-Durocher *et al.*, 2010) (Fig 1) among 88 others. Prior to Boltzmann-Arrhenius model fitting, we took the inverse of all responses to temperature where the unit in the response was time (e.g. gut clearance time). 89 out of 94 activation energies reported here characterize processes that occur in all lakes, all year round, and both at the surface and at the bottom of lakes. A full list can be found in dataset supplement S1.

Prior to substituting temperature profile data into Boltzmann-Arrhenius equations, temperature data were interpolated to create a continuous record with a daily time step. To interpolate the temperature time series, first, data were deseasonalized separately for each depth in each lake. To deseasonalize the temperature data, we began by pooling them by day of year for a specific depth over the entire temperature time series for each lake. The seasonality of the temperature cycle at each depth was calculated as the difference between the 30-day running mean temperature for each day of the year and the grand mean across all days of the year. This date-specific seasonal variation was subtracted from each raw temperature measurement to yield a deseasonalized dataset. The deseasonalized dataset was then linearly interpolated from the beginning to end of any data gaps to yield a continuous daily time series. Finally, the seasonal temperature variation was re-added to obtain an interpolated time series informed by all available data at a particular depth. We carried out this procedure separately for the uppermost and lowermost temperature measurements in each lake. To determine whether the 26 lakes with annualized data were representative of the broader population of lakes, we calculated summer averages following the methods of (Schneider & Hook, 2010) from the 26 lakes with annual data.

Average summer surface temperatures

Average summer surface temperature data from 271 lake monitoring sites located in arctic, boreal, temperate, subtropical, and tropical regions were extracted from a published data source (Sharma *et al.*, 2015) and also used to estimate change in metabolic traits through time. These temperature data are available for the period 1985-2009 and includes both remote sensing and in situ measurements in order to represent the spatial distribution and physical characteristics of lakes around the world. Each of these 271 lakes had at least 12 years of summer mean surface temperature data over the study period. “Summer” was defined as the period from July 1 through September 30 for lakes in northern hemisphere and January 1 through March 29 for lakes in the southern hemisphere. Some large, multi-basin lakes had up to 3 monitoring sites within them in recognition of the substantial amount of within-lake variation in warming rates in some lakes (Kraemer *et al.*, 2015a).

As we had done with temperature profile data, we substituted time series of lake average surface temperatures from each site into general Boltzmann-Arrhenius equations relating seven metabolic rates to temperature. We interpret output of these calculations as an estimate of each metabolic rate at the lake’s average summer surface temperature for a given year. While using year-round temperature data would be ideal, such time series are not available for most lakes. As a consequence of using average summer surface temperature data, these estimates do not represent the average metabolic rate over the entire summer, as such extrapolations would violate the fallacy of the average (Savage, 2004). Rather, they should be interpreted as an estimate of a given metabolic trait when the lake temperature is at its summer average.

Trend Analysis

We analyzed long-term trends in lake temperatures and in metabolic traits using Theil-Sen nonparametric regression (Theil, 1950). To enable comparison across traits of different activation energies with different units, we express the rate of change over time for each metabolic trait as a proportion of the estimated trait at 15°C. To test whether lake warming rates and lake temperatures were correlated across lakes, we calculated Spearman's correlation coefficients separately for each temperature data source. All statistics were run using the R statistical computing environment (R Development Core Team, 2013).

Results

Geography of lake temperature

Average lake temperatures based on 271 globally distributed lakes varied predictably across the globe. High latitude and high elevation lakes were typically cooler than low latitude and low elevation lakes. The earth's two subtropical high pressure zones coincided with relatively low lake temperatures on average than would be expected at these latitudes due to the dominance of relatively cold, high-elevation lakes there. The range of average lake temperatures depended on lake depth and season. Average summer surface temperatures had a wider range (3.81 - 31.49 °C) and higher median (20.23 °C) than either annualized lake surface temperatures (range: 1.14 - 26.35 °C, median: 11.40 °C) or annualized lake bottom temperatures (range: 1.76 – 25.01 °C, median: 5.17 °C) (Fig 2).

Geography of lake warming rates

Average summer surface temperatures increased by 0.36 °C decade⁻¹ over the period from 1985 to 2009 based on lake temperature data from 271 lake monitoring sites around the world (Fig 2). Of the 271 lakes in this analysis, 233 showed warming trends based on average

summer surface temperature data (positive Theil-Sen slopes). The warming trend was significant in 123 of the 233 lakes with positive warming trends (Mann-Kendall, $p < 0.1$). Of the 38 lakes with cooling trends (negative Theil-Sen slopes), only 2 trends were significant (Mann-Kendall, $p < 0.1$). Lake warming rates were negatively correlated to average summer lake temperature ($r = -0.21$, $p < 0.001$) (Fig 3).

Average annual surface temperature has increased by $0.29 \text{ }^\circ\text{C decade}^{-1}$ over the period from 1970-2010 for the 26 lake monitoring sites with annual profile data (Fig. 2). Of these 26 lake monitoring sites, all 26 were warming (positive Theil-Sen slopes), and 20 of those showed significant warming trends (Mann-Kendall, $p < 0.1$). Average annual bottom temperature data have increased by only $0.04 \text{ }^\circ\text{C decade}^{-1}$ over the period from 1970-2010 on average. 18 of 26 lake monitoring sites with temperature profiles had increasing bottom temperatures (positive Theil-Sen slopes) but the increase was significant (Mann-Kendall, $p < 0.1$) in only 10 of these lakes. Eight lakes had cooling bottom temperature trends, two of which were significant (Mann-Kendall, $p < 0.1$). In contrast to summer average surface warming, annualized surface warming and annualized bottom warming were only weakly correlated to average lake temperatures (surface $r = -0.01$ and $p = 0.96$, bottom $r = -0.19$ and $p = 0.35$) (Fig 3).

Metabolic responses to warming

Freshwater activation energies reported here span a range from 0.005 eV (effective temperature independence) to 2.56 eV (high temperature sensitivity) (Fig 1). The mean and median activation energies were 0.57 eV and 0.481 eV, respectively, indicating slight skewness (Fig 1). Using the median activation energy to calculate metabolic change through time, we expect metabolic traits at the surfaces of lakes to increase by a factor of $0.019 \cdot \nu_{15^\circ\text{C}} \text{ decade}^{-1}$,

where $v_{15^{\circ}\text{C}}$ is the estimated metabolic response at 15 °C (Fig 3). Also using the median activation energy, we expect metabolic responses at the bottom of lakes to change more slowly than at lake surfaces ($0.004 * v_{15^{\circ}\text{C}} \text{ decade}^{-1}$) due to slower warming rates there on average (Fig 3). The median metabolic response based on summer surface average temperatures was higher than annualized surface temperatures ($0.036 * v_{15^{\circ}\text{C}} \text{ decade}^{-1}$) where temperatures are warming faster on average from higher starting point (Fig 2).

There was extraordinary variation in the estimated direct effects of temperature on metabolism across metabolic responses with different activation energies. The average metabolic response to warming for the metabolic response with the lowest activation energy (0.005 eV) was less than $0.001 * v_{15^{\circ}\text{C}} \text{ decade}^{-1}$ averaged across lakes based on annualized lake surface temperature. However, the average metabolic response to warming with the highest activation energy was $1.160 * v_{15^{\circ}\text{C}} \text{ decade}^{-1}$ when based on annualized surface warming.

For the bulk of activation energies analyzed here, metabolic responses to warming were greatest for lakes with high average temperatures (Fig 4). This pattern held true even when low temperature lakes were warming faster on average than high temperature lakes (Fig 4). For instance, Lake Superior is one of the top five fastest warming lakes on the planet, but its median metabolic response is only in the 63rd percentile due to its low average temperature. Metabolic responses in warm lakes were more sensitive to temperature change than cold lakes especially when metabolic responses had high activation energies (Fig 4). However, at the lowest activation energies, metabolic responses were greater in cold lakes than in warm lakes across all temperature data sources used (Fig 4). The point where cold lakes switched from having larger metabolic responses to having lower responses occurred below the median activation energy and well below the mean activation energy for metabolic responses in lakes (Fig 4). This switching

point varied depending on depth and season. The activation energies where the switches occurred were 0.425 eV (summer average surface temperature), 0.057 eV (annualized surface temperature), 0.208 eV (annualized bottom temperature) (Fig 4). This variation in switching points appear to be most related to the strength of the correlation between average temperatures and warming rates. When the correlation between temperature and warming rates is most negative (as is the case with summer surface average temperature and warming rates), the range of activation energies over which warm lake metabolic responses exceeded cold lake responses is smallest (Fig 4).

Discussion

Our findings suggest that global patterns in the response of lake ecosystems to climate change are linked to the kinetics of the chemical reactions underlying those responses. The bulk of metabolic responses show larger absolute changes in warm lakes even when warm lake temperatures are warming more slowly than cold lakes. However, traits with low activation energies (e.g. fish metabolism, gross primary production) tended to show larger absolute rate changes in cold lakes in parallel with warming rates especially when average lake temperature and warming rates were negatively correlated (Fig 4). Thus, activation energies provide a simple heuristic for predicting both where and why metabolic consequences of warming do not parallel warming rates.

Geography of temperature and warming rates

The surfaces of relatively cold lakes were warming faster than warm lakes in the summer, agreeing with previous findings based on satellite-derived surface temperatures of large lakes (Schneider & Hook, 2010). This pattern was observed when we used summer average data from

271 lakes and also when we used summer average data from the 26 lakes where annual temperature data were available. Global patterns in lake warming rates represent the intersection of global and regional climatic drivers with local lake conditions (O'Reilly *et al.* 2015, in press). Variability in lake warming rates across the globe has been explained by a number of factors including cloud cover, solar radiation, the presence or absence of lake ice, and air temperature (O'Reilly *et al.* 2015, in press).

In contrast to summer surface warming rates, annualized warming rates were not strongly related to average lake temperature. This result suggests that the mechanisms that drive variability in summer surface warming may be outweighed by other factors at other times of the year. Thorough characterization of annualized lake warming rates across the globe will require the addition of many more long-term lake monitoring sites in the tropics than are currently operational. Satellite-based estimates may help circumvent the latitudinal bias in lake surface temperature monitoring. But, given the strong difference between metabolic responses estimated here for lake surfaces and lake bottoms (Fig 3), surface temperature change alone may be a poor indicator of lake-wide metabolic responses. For this reason, satellite based lake surface temperature still give a limited representation of temperature change in lakes and will not be able to circumvent the need for more long-term in situ temperature monitoring in the tropics.

Activation energies as a heuristic

Responses to lake warming will be disproportionate to warming rates themselves for most metabolic responses to temperature. This corroborates other work that showed that metabolic impacts of warming on terrestrial ectotherms may be greatest in the tropics despite lower air temperature warming rates there (Dillon *et al.*, 2010). However, generalizations about

nonlinear responses to temperature always being disproportionate to warming rates are not justified. This is because the temperature dependent metabolic responses with low activation energies (e.g. gross primary production and fish metabolism) will parallel global patterns of warming rates in lakes. The difference between our conclusions and that for terrestrial ectotherms is attributable to the inclusion of a broader range of metabolic responses including those with low activation energies.

Our findings have applications for predicting whether the metabolic responses for other biological responses with different activation energies than those included in our analyses will be disproportionate to warming rates. We identified critical transition points where warm lakes switched from having lower to having higher metabolic responses than cold lakes. This critical transition point varied by season and by lake depth. The critical transition point increased for summer surface temperatures where there was a strong negative correlation between temperature and warming rates. This suggests that relatively high warming in lakes with cold average temperatures counteracts the nonlinearity of metabolic responses and affects global patterns in metabolic responses. Other ecosystem types where there is a strong negative correlation between temperature and warming rates, as in terrestrial ecosystems, are most likely to have metabolic responses that parallel warming rates.

Due to the decrease in warming rate at depth in many lakes (Winslow et al 2014, Kraemer et al 2015), absolute biological responses to temperature depend heavily on the depth where each process is concentrated. The disparity between surface temperature trends and bottom temperature trends reflects differences in the factors affecting temperature at different depths in lakes. Lake surface temperatures are determined predominantly by direct heat exchange across the air-water interface and are hence correlated with air temperature on many

timescales (Livingstone & Lotter, 1998; Livingstone, 2003), whereas the temperature of deeper water is determined to a large extent by lake mixing behaviour (Livingstone David *et al.*, 1993; Livingstone, David *et al.*, 1997; Ambrosetti & Barbanti, 1999). While 89 out of 94 of the activation energies reported here characterize processes that occur throughout lakes, several key metabolic responses are localized. For instance, gross primary production occurs near the surface of lakes where light is most available and where metabolic responses to warming are most likely to parallel warming rates. However, responses that occur primarily in the anoxic benthos of lakes (e.g. methanogenesis), are least likely to parallel variation in lake warming rates.

Distinguishing fundamental and apparent activation energies

We have focused on estimating the direct effect of temperature rise on metabolic responses. However, the actual change in metabolism through time as a result of climate change will depend on the sum of direct and indirect effects of temperature on metabolism as well as the effects of independent temperature covariates. For instance, climate warming-driven shifts in lake mixing could affect lake metabolism but is not accounted for in our analysis. Incorporating all direct and indirect effects of climate change into models of lake metabolism will be required to generate accurate estimates of changes in metabolism through time. This is especially the case for metabolic responses that have large standard deviations in site-specific activation energy (e.g. 0.59 eV standard deviation for methane emissions across sites) (Yvon-Durocher *et al.*, 2014). There is a strong need to evaluate whether variability in site specific activation energies can be explained by site traits. In some cases, ecological differences between sites (e.g. organic carbon recalcitrance, nutrient stoichiometry, community structure, local adaptation) may constrain or amplify the apparent sensitivity of metabolic responses to temperature change (Yvon-Durocher *et al.*, 2014). Thus, site-specific conditions could dampen or amplify the underlying temperature

dependence of a specific metabolic response (Jankowski *et al.*, 2014). At present, there is no evidence that site-specific activation energies vary systematically across the globe (Perkins *et al.*, 2012; Yvon-Durocher *et al.*, 2012, 2014). In our compilation of freshwater activation energies, we found no significant relationship between activation energy and the average temperature over which activation energy was calculated or with whether they were measured in the laboratory or in the field. However, activation energies for tropical metabolic responses to temperature continue to be underrepresented in our data compilation, underscoring an acute need for further assessment of site-specific activation energies in the tropics. A better understanding of drivers of site-specific activation energies would enable more accurate estimates of the effect of climate change on lake metabolism at the global scale. But site specific activation energies reflecting direct and indirect effects of temperature on metabolism are not likely to substantially alter the general patterns suggested by our analyses regarding the direct effects of temperature alone.

Consequences of metabolic acceleration

Our calculations suggest that the direct effect of climate warming on lakes has been to accelerate metabolism. Higher rates of organismal, population, community, and ecosystem metabolism estimated here have likely altered the functioning of lake ecosystems. Higher metabolic rates may increase the vulnerability of fish and other ectotherms to starvation unless food resources increase commensurately (Dillon *et al.*, 2010; Cheung *et al.*, 2012). The relative increase in lake primary production estimated here is 1.2% lower, on average, than the increase in ecosystem respiration, suggesting that food availability may decline relative to its demand (Yvon-Durocher *et al.*, 2010). Increases in metabolic demands of organisms estimated here also assume that these organisms will acclimate to their new thermal environment. If behavioral and physiological acclimation are not possible, the impacts of warming on organisms could be

dampened or amplified. Maintenance of metabolic stasis through relocation to deeper, colder water has been invoked as an adaptation strategy for aquatic ectotherms in the face of environmental temperature change (Cheung *et al.*, 2012; Burrows *et al.*, 2014); however, such forced shifts may raise a host of new problems by separating aquatic fauna from habitats whose depth distribution is constrained by light and nutrient gradients (Cheung *et al.*, 2012).

Understanding the consequences of metabolic acceleration for lake ecosystems is critical for predicting shifts in the benefits that lakes provide to society. The lakes included in this analysis are globally significant repositories of freshwater biodiversity and ecosystem services (Millennium Ecosystem Assessment, 2005). In aggregate, they contain the vast majority of liquid surface freshwater on the planet. The large ancient lakes in our analysis (Tanganyika, Hovsgol, Baikal, Biwa, Kinneret, Van, Valencia, Titicaca, etc.) hold thousands of animal species found nowhere else on Earth (Vadeboncoeur *et al.*, 2011). The African rift lakes support highly productive fisheries that are vital to regional economies and food security (*UN Water Report: Water Monitoring, Mapping Existing Global Systems & Initiatives*, 2006). Lakes Tahoe and Zurich are deeply integrated into regional economies through recreation and tourism. The consequences of metabolic acceleration for biodiversity and ecosystem services in lakes will also depend on shifts in lake physics (Kraemer *et al.*, 2015b), the global distribution of lake area (Lewis, 1987), and complex ecological interactions that are beyond the scope of this study. However, our work suggests that substantial metabolic acceleration has already occurred since 1970, and is most pronounced in the tropics where human well-being and freshwater biodiversity may be most affected.

Conclusion

Joint consideration of global patterns of baseline temperatures and warming rates indicates that warming has had greater absolute direct effects on warm lake ecosystems than cold lake ecosystems for most temperature dependent metabolic responses in the world's lakes. The extent to which metabolic responses to warming will parallel warming rates in other ecosystem types will depend on their activation energy and whether temperature and warming rates are correlated over broad spatial scales in those ecosystems. Like analyses of climate velocity (Loarie *et al.*, 2009; Burrows *et al.*, 2014), climate novelty (Williams *et al.*, 2007), and the thermal tolerances of organisms (Ghalambor *et al.*, 2006; Deutsch *et al.*, 2008; Tewksbury *et al.*, 2008; Huey & Kingsolver, 2011), our findings demonstrate that patterns in warming rates alone can be misleading as predictors of organismal or ecosystem responses to climate change (Fig 4). For the critical biological processes analyzed herein, activation energies provide a powerful basis for understanding such decoupling and the resulting counterintuitive patterns of metabolic responses to temperature change.

Acknowledgements

We are grateful for field research funding from the National Science Foundation (NSF) (DEB-1030242 and DEB-0842253), and encouragement from the Global Lake Temperature Collaboration (DEB-1147666, National Aeronautics and Space Administration (NASA), Research Opportunities in Space and Earth Sciences (ROSES) Grant, Institute of Agricultural and Natural Resources (IANR), University of Nebraska-Lincoln). Thank you to several anonymous reviewers for constructive feedback.

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Supporting Information:

Dataset S1: Activation energies and data sources for 94 freshwater activation energies used in our study.

Response	Activation Energy (eV)	Sites/ Species	Source
Attack Probability	1.79	3	(Dell <i>et al.</i> , 2013)
Attack-Field Encounter Density Rate	0.78	3	(Dell <i>et al.</i> , 2013)
Attack-Field Encounter Rate	0.5	4	(Dell <i>et al.</i> , 2013)
Attack-Field Reaction Probability	0.72	3	(Dell <i>et al.</i> , 2013)
Average lifespan	0.46	30	(Munch & Salinas, 2009)
Chlorophyll-a-Specific Carbon Production Rate	0.48	1	(Dell <i>et al.</i> , 2013)
Community-level rate of CH ₄ production	0.93	47	(Yvon-Durocher <i>et al.</i> , 2014)
Critical Holding Velocity	0.33	3	(Dell <i>et al.</i> , 2013)
Critical Travel Velocity	0.34	15	(Dell <i>et al.</i> , 2013)
Critical Travel Velocity 50%	0.24	3	(Dell <i>et al.</i> , 2013)
Development Time	0.57	2	(Dell <i>et al.</i> , 2013)
Digestion Time 50%	0.77	2	(Dell <i>et al.</i> , 2013)
Digestion Time 75%	0.83	5	(Dell <i>et al.</i> , 2013)
Digestion Time 90%	0.76	5	(Dell <i>et al.</i> , 2013)
Digestion Time 99%	0.76	5	(Dell <i>et al.</i> , 2013)
Ecosystem-level CH ₄ emission	0.96	127	(Yvon-Durocher <i>et al.</i> , 2014)
Ecosystem-level CH ₄ :CO ₂ emission ratio	0.71	38	(Yvon-Durocher <i>et al.</i> , 2014)
Ecothermic vertebrate attack rate	0.51	115	(Rall <i>et al.</i> , 2012)
Ecothermic vertebrate handling time	0.28	115	(Rall <i>et al.</i> , 2012)
Escape Angular Rate of Body Turning	0.23	4	(Dell <i>et al.</i> , 2013)
Escape Body Acceleration	0.12	1	(Dell <i>et al.</i> , 2013)
Escape Body Velocity	0.25	31	(Dell <i>et al.</i> , 2013)
Escape Muscle 50% Relaxation Time	0.38	3	(Dell <i>et al.</i> , 2013)
Escape Muscle 50% Twitch Time	0.41	3	(Dell <i>et al.</i> , 2013)
Escape Muscle Peak Twitch Time	0.38	3	(Dell <i>et al.</i> , 2013)
Escape Stroke Length	0.03	2	(Dell <i>et al.</i> , 2013)
Escape Stroke Rate	0.08	11	(Dell <i>et al.</i> , 2013)
Escape Tail Beat Rate	0.25	2	(Dell <i>et al.</i> , 2013)
Faecal Excretion Rate	0.34	3	(Dell <i>et al.</i> , 2013)
Filtration Rate	0.62	4	(Dell <i>et al.</i> , 2013)
Fish respiration	0.41	113	(Gillooly <i>et al.</i> , 2001)
Fish swimming metabolic cost of transport	0.19	29	(Hein & Keirsted, 2012)
Fixed-point Activity Rate	0.16	1	(Dell <i>et al.</i> , 2013)
Foraging Submergence Duration	1.77	2	(Dell <i>et al.</i> , 2013)
Foraging Submergence Time	1.35	2	(Dell <i>et al.</i> , 2013)
Foraging Velocity	0.44	4	(Dell <i>et al.</i> , 2013)
Grazing Rate	0.01	1	(Dell <i>et al.</i> , 2013)
Gross primary production	0.45	1	(Yvon-Durocher <i>et al.</i> , 2012)
Gut Loading Time	0.48	1	(Dell <i>et al.</i> , 2013)
Gut Passage Time	0.43	2	(Dell <i>et al.</i> , 2013)
Handling Duration	0.67	2	(Dell <i>et al.</i> , 2013)
In Vitro Gill Beat Rate	0.51	2	(Dell <i>et al.</i> , 2013)

In Vitro Muscle 50% Relaxation Time	0.43	6	(Dell <i>et al.</i> , 2013)
In Vitro Muscle Contraction Duration	0.15	3	(Dell <i>et al.</i> , 2013)
Individual Length Growth Rate	1.12	2	(Dell <i>et al.</i> , 2013)
Individual Mass Growth Rate	2.56	1	(Dell <i>et al.</i> , 2013)
Instantaneous Digestion Mass Rate	1.12	4	(Dell <i>et al.</i> , 2013)
Invertebrate attack rate	0.53	154	(Rall <i>et al.</i> , 2012)
Invertebrate handling time	0.42	154	(Rall <i>et al.</i> , 2012)
Invertebrate respiration	0.74	20	(Gillooly <i>et al.</i> , 2001)
Lake benthic ecosystem respiration	0.55	27	(Yvon-Durocher <i>et al.</i> , 2012)
Lake Pelagic ecosystem respiration	0.63	95	(Yvon-Durocher <i>et al.</i> , 2012)
Longevity	0.46	1	(Dell <i>et al.</i> , 2013)
Mass-scaled amphibian embryonic development time	0.14	34	(Gillooly <i>et al.</i> , 2002)
Mass-scaled fish embryonic development time	0.13	59	(Gillooly <i>et al.</i> , 2002)
Mass-scaled multicellular eukaryote population growth rate	0.84	57	(Savage <i>et al.</i> , 2004)
Mass-scaled multivoltine aquatic insects embryonic development time	0.12	35	(Gillooly <i>et al.</i> , 2002)
Mass-scaled Post-embryonic development time for zooplankton	0.11	103	(Gillooly <i>et al.</i> , 2002)
Mass-scaled unicellular eukaryote population growth rate	0.54	14	(Savage <i>et al.</i> , 2004)
Mass-scaled vertebrate population growth rate	0.35	9	(Savage <i>et al.</i> , 2004)
Mass-scaled zooplankton embryonic development time	0.11	96	(Gillooly <i>et al.</i> , 2002)
Mass-Specific Ammonia Excretion Rate	1.1	1	(Dell <i>et al.</i> , 2013)
Mass-Specific Consumption Rate	1.99	3	(Dell <i>et al.</i> , 2013)
Mass-Specific Escape Inertial Hydrodynamic Power Requirement	0.65	11	(Dell <i>et al.</i> , 2013)
Mass-Specific Mass Clearance Rate	0.4	2	(Dell <i>et al.</i> , 2013)
Mass-Specific Mass Consumption Rate	0.51	1	(Dell <i>et al.</i> , 2013)
Mass-Specific Oxygen Mass Scope For Activity	0.16	2	(Dell <i>et al.</i> , 2013)
Mass-Specific Respiration Rate	0.67	1	(Dell <i>et al.</i> , 2013)
Maximum lifespan	0.6	43	(Munch & Salinas, 2009)
Molting Frequency	0.59	1	(Dell <i>et al.</i> , 2013)
Mortality Rate	0.14	3	(Dell <i>et al.</i> , 2013)
Net Primary production	0.41	1	(Yvon-Durocher <i>et al.</i> , 2012)
Photosynthesis	0.3	1	(Yvon-Durocher <i>et al.</i> , 2012)
Point-Encounter Rate	0.71	2	(Dell <i>et al.</i> , 2013)
Population Filter-Feeding Probability	0.02	7	(Dell <i>et al.</i> , 2013)
Population Growth Rate	0.53	9	(Dell <i>et al.</i> , 2013)
Population Size	0.37	1	(Dell <i>et al.</i> , 2013)
Population Voluntary Exposure Probability	1.1	2	(Dell <i>et al.</i> , 2013)
Population Voluntary Movement Probability	1.45	3	(Dell <i>et al.</i> , 2013)
Population Voluntary Movement Probability of Exposed Individuals	0.29	1	(Dell <i>et al.</i> , 2013)
Population-level rate of methanogenesis	1.1	33	(Yvon-Durocher <i>et al.</i> , 2014)
Resource Consumption Rate	0.57	71	(Dell <i>et al.</i> , 2013)

Resource Mass Consumption Rate	0.5	28	(Dell <i>et al.</i> , 2013)
Strike-Field Encounter Rate	0.53	4	(Dell <i>et al.</i> , 2013)
Subjugation-through-Consumption Duration	0.83	1	(Dell <i>et al.</i> , 2013)
Successful Attack Probability	0.23	3	(Dell <i>et al.</i> , 2013)
Survival Time	0.41	2	(Dell <i>et al.</i> , 2013)
'Swim Underwater' Defence Probability	0.51	1	(Dell <i>et al.</i> , 2013)
Undigested Mass	1.4	10	(Dell <i>et al.</i> , 2013)
Unicell respiration	0.71	30	(Gillooly <i>et al.</i> , 2001)
Voluntary Body Velocity	0.29	42	(Dell <i>et al.</i> , 2013)
Voluntary Moving Probability	0.11	4	(Dell <i>et al.</i> , 2013)
Voluntary Stroke Rate	0.33	27	(Dell <i>et al.</i> , 2013)
Voluntary Tail Beat Rate	0.38	1	(Dell <i>et al.</i> , 2013)

Text S2: Temperature Data Sources. Signy Island lake (lakes Heywood, Moss, Sombre)

temperature data were contributed by the Polar Data Centre under a British Open Government License, British Antarctic Survey, 1963-2004 (GB/NERC/BAS/AEDC/00063)

(http://www.antarctica.ac.uk/bas_research/data/access/index.php). Long-term temperature data from Lake Tanganyika are available through DATAOne and LTER data portals. Lake Kivu data were supplied by Francois Darchambeau, Jean-Pierre Descy, Alberto Vieira Borges, and Martin Schmid and funded by the ARES-CCD through the “ECOSYKI : Studies on Lake Kivu ecosystem for its sustainable management” project, by the Belgian Federal Science Policy Office through the “EAGLES: East African Great Lake Ecosystem Sensitivity to Changes” (EAGLES, SD/AR/02A) project, and by the Fonds National de la Recherche Scientifique (Belgium) through the “CAKI: Cycle du Carbone et des Nutriments au Lac Kivu” and “MICKY: Microbial Diversity and Processes in Lake Kivu” projects (data contact: Jean-Pierre Descy, jpdescy@gmail.com) . Lake Tahoe temperature data collection has been funded by the Tahoe Regional planning Agency, Lahontan Regional Water Quality Board and contributed by the UC-Davis Tahoe Environmental Research Center (data available at <http://terc.ucdavis.edu/>). Lake Atitlan temperature data collection was funded by UVG and USAID (data contact: Margaret Dix,

margeret.dix@gmail.com). Lake Baikal temperature data collection was partially funded by the Russian Ministry of Education and Science, (GR 01201461929) (data contact: Eugene Silow, eugenesilow@gmail.com). Data from Toolik Lake, Lake Mendota, and Trout Lake were provided by the National Science Foundation's Long-Term-Ecological Research program (data sets titled, North Temperate Lakes LTER: Physical Limnology of Primary Study Lakes, Physical and chemical data for various lakes near Toolik Research Station, Arctic LTER, <http://www.lternet.edu/lter-sites>). Lake Kinneret temperature data were accessed through the Yigal Allon Kinneret Limnological Laboratory (data available through the Lake Kinneret Data Center, <http://www.ocean.org.il/Eng/KinneretDataCenter/ProfileDC.asp>). Data from Lake Zurich were provided by the City of Zurich Water Supply (WVZ). Data from Greifensee were provided by the Amt für Abfall, Wasser, Energie und Luft, Canton of Zurich. Data contact for lakes Zurich and Greifensee is David Livingstone, David.Livingstone@eawag.ch. Data from Lake Geneva were from SOERE OLA-IS, INRA Thonon-les-Bains, CIPEL, [downloaded on January 2014], developed by Eco-Informatics ORE INRA Team (data contact: Orlane Anneville, orlane.anneville@thonon.inra.fr). Lake Biwa data were shared by Akihiko Oyama (gf30@pref.shiga.lg.jp) of the Shiga Prefectural Fishery Experiment Station. Data for lakes Rawson, 227, and 302 were contributed by the Experimental Lakes Area of Fisheries and Oceans-Canada (data freely available after signing data use agreement at www.experimentallakesarea.ca). Data from Castle Lake were contributed by the Aquatic Ecosystems Analysis Laboratory, University of Nevada-Reno (data contact: Sudeep Chandra, limnosudeep@me.com). Lake Nkugute data are from "CLANIMAE" report: Science for Sustainable Development, 2010 (<http://www.belspo.be/belspo/ssd/science/Reports/CLANIMAE%20FinRep%20PH%201.pdf>).

Summer mean annual surface temperatures from 1985-2009 are available for the lakes in this analysis at doi:10.1038/sdata.2015.8.

Figures:

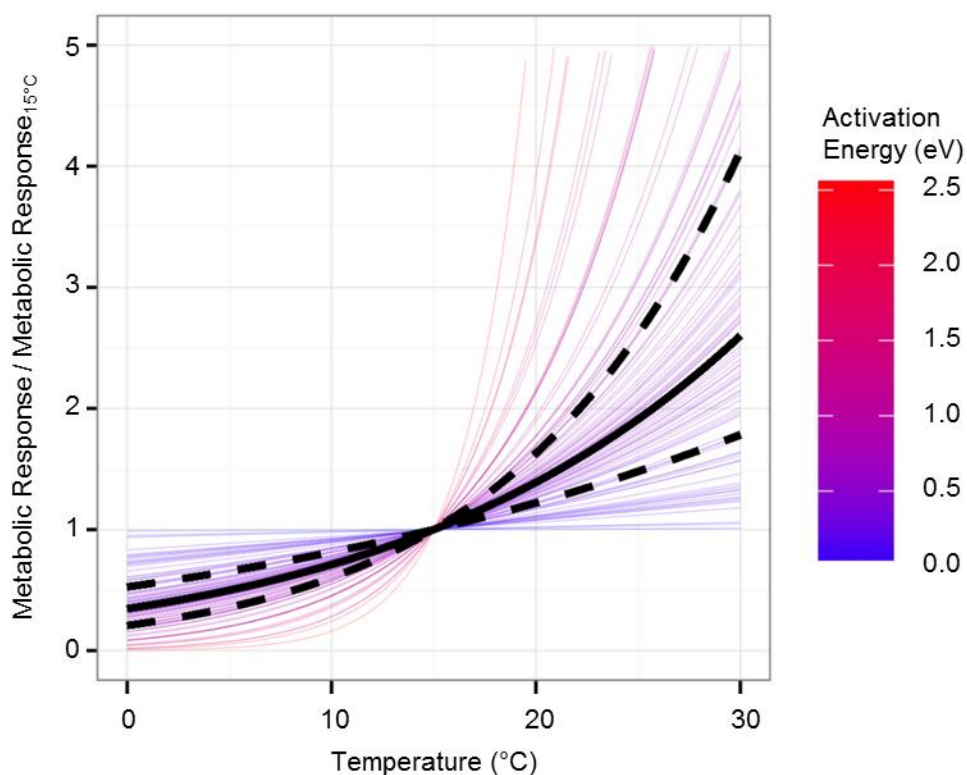


Figure 1: Exponential temperature-dependence of biological process rates in lakes. Nonlinear temperature dependencies were based on the Boltzmann-Arrhenius factor with activation energies specific to each biological process. Nonlinear temperature dependencies are illustrated here as a proportion of the rate estimated for 15° C. The steepness of the curve is related to the activation energy of each biological process; the higher the activation energy, the steeper the curve.

Annual Lake Bottom Temperature
Annual Lake Surface Temperature
Summer Lake Surface Temperature

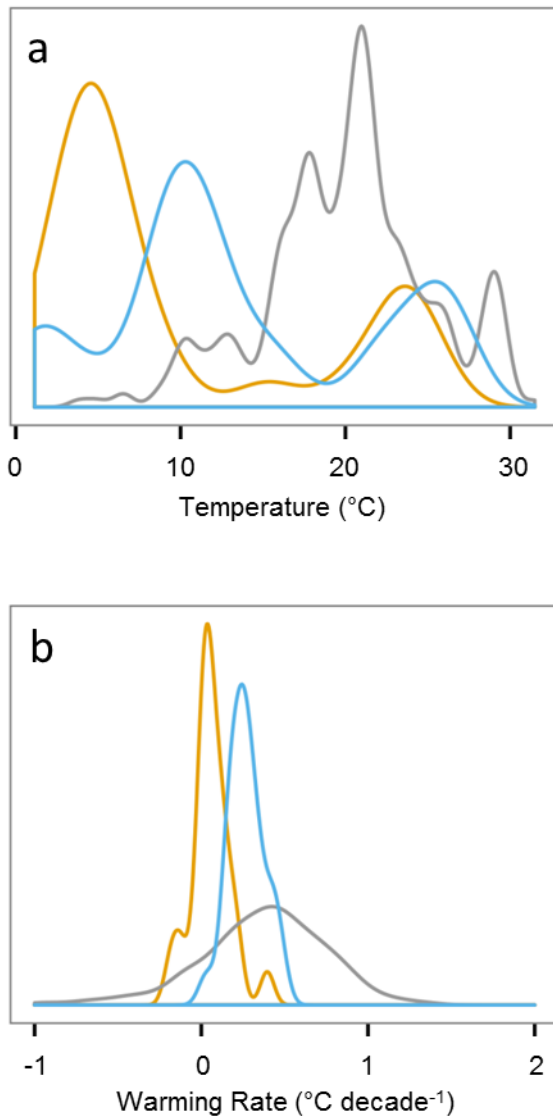


Figure 2: Distribution of lake average temperatures (a) and lake warming rates (b) based on three different temperature sources: average summer surface temperatures (grey), annual surface temperatures (blue), and annual bottom temperatures (orange).

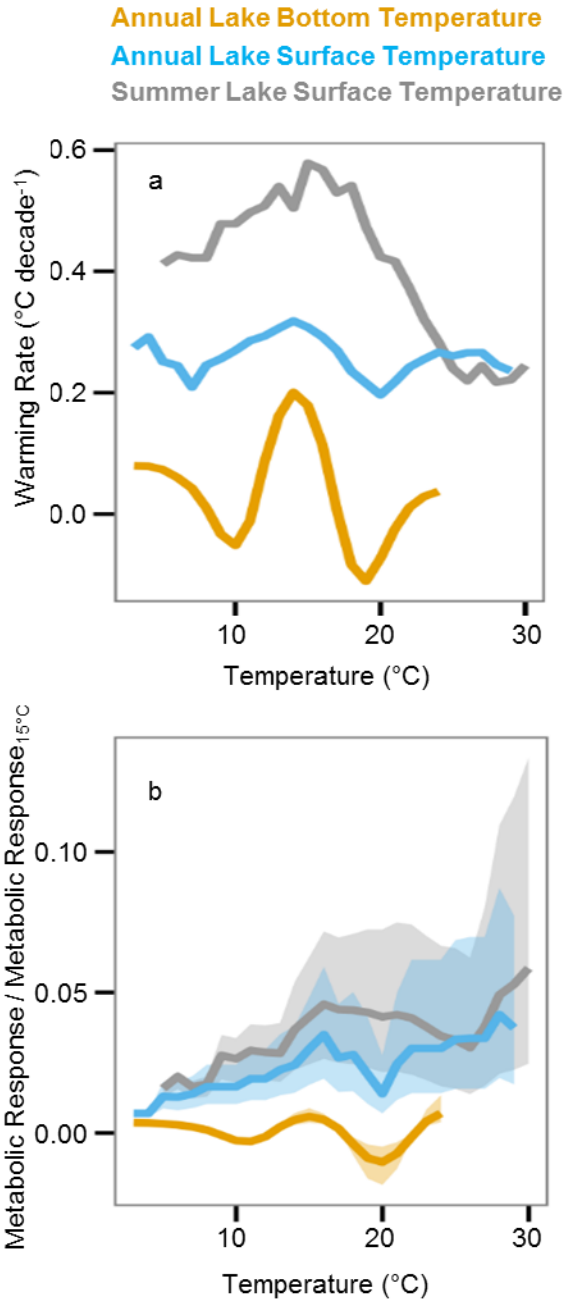


Figure 3: Warming rate (a) and metabolic responses (b) as a function of average lake temperature. Warming rates and metabolic responses are split by temperature data types: average summer surface temperatures (grey), annual surface temperatures (blue), and annual bottom temperatures (orange). Lines in panel (b) indicate the metabolic response for the median

activation energy. Colored ribbons in panel (b) indicate range of metabolic responses between the first and third quartiles (see Fig 1) of the distribution of activation energies used in our study.

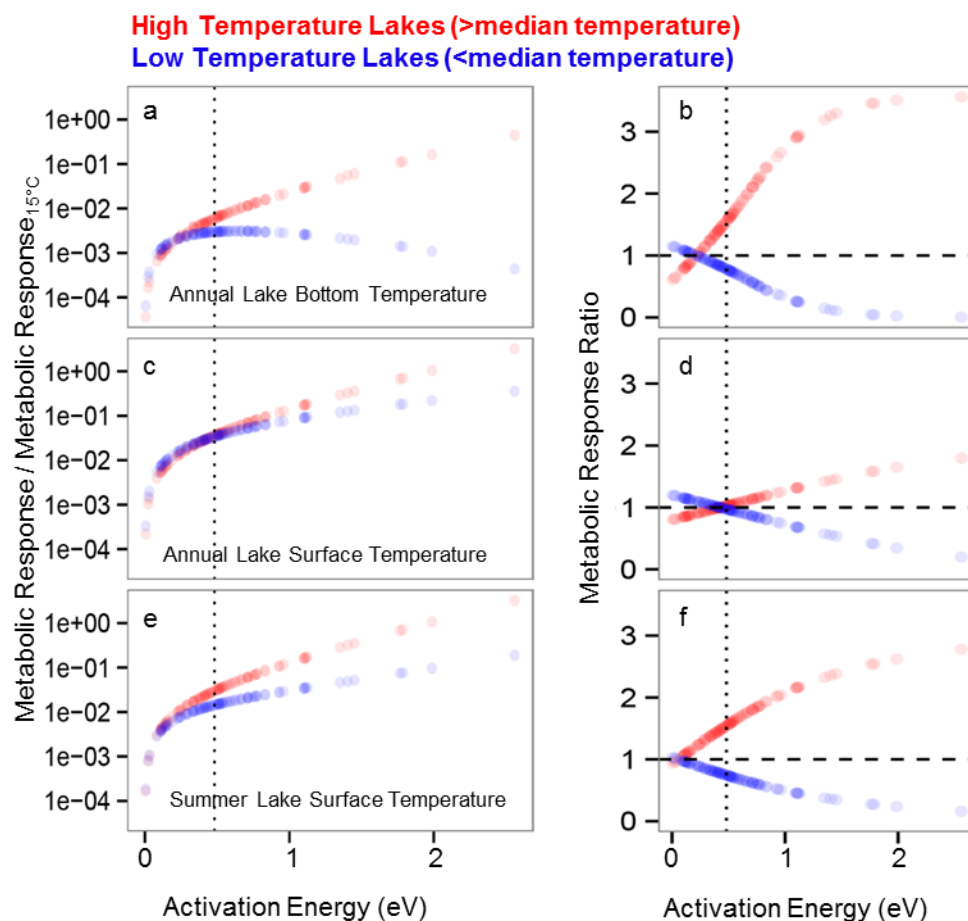


Figure 4: Average metabolic responses for warmest 50% of lakes (red) and coldest 50% of lakes (blue) as a function of activation energy. Warming rates and metabolic responses are split into separate panels by temperature data types used in their estimation: annual bottom temperatures (a, b), annual surface temperatures (c, d), average summer surface temperatures (e, f). Panels a, c, and e show the estimated change in each metabolic response scaled to the estimated rate at 15°C. Panels b, d, f show the metabolic responses divided by the global average metabolic response for its activation energy to facilitate comparison between warm and cold lakes. The vertical dashed line indicates the median activation energy. The point where the implied blue and

red lines cross indicates the activation energy where warm lakes switch from having smaller to having larger metabolic responses to warming.

Chapter 4: Warming reduces ecosystem and organism metabolism in Africa's deepest lake*

Abstract

Climate warming is predicted to accelerate ecosystem and organism metabolism due to the fundamental temperature dependence of biochemical kinetics. However, the direct influence of temperature on metabolism can be outweighed by warming's indirect influences—potentially causing metabolic rates to decrease with temperature. Here we show that in Lake Tanganyika, ecosystem metabolic rates (pelagic primary production, pelagic ecosystem respiration, littoral primary production, littoral ecosystem respiration) and the metabolic rates of some endemic species of fish (respiration, ammonium excretion, soluble reactive phosphorus excretion) are negatively related to temperature on seasonal timescales. The negative relationship between organismal and ecosystem metabolism arises from warming-induced shifts in lake mixing which diminish lake productivity and food availability for fishes. Metabolic declines brought about by warming may be widely observed in other nutrient-poor lakes where lake mixing is a key source of nutrients to the photic zone.

Introduction

The metabolic theory of ecology predicts that organismal and ecosystem metabolism is directly linked to temperature due to the fundamentals of biochemical kinetics (Gillooly et al. 2001, Yvon-Durocher et al. 2010, Dell et al. 2011). Within their optimal range, organisms and ecosystems operating at higher temperatures are expected to have higher metabolic rates in proportion to the Boltzmann-Arrhenius factor,

* To be submitted for publication with Cortney Morris, Lesley Yu-Jung Kim, Ellen Hamann, Yvonne Vadeboncoeur, Peter B. McIntyre as potential co-authors

$$v \propto e^{-E_a/kT}$$

where v is the reaction rate, E_a is the activation energy, k is the Boltzmann constant, and T is the temperature in Kelvin. Boltzmann-Arrhenius model fitting of metabolism at the organismal, population, community, and ecosystem scale have demonstrated that the metabolic theory of ecology has broad importance for explaining pattern and process in nature (Gillooly et al. 2001, Dell et al. 2011, Yvon-Durocher et al. 2012).

The ubiquity of temperature dependence in nature has implications for the direct effect of climate warming on the environment. Estimations of the temperature sensitivity of metabolism have been used widely to model global scale ecosystem responses to warming (Allen et al. 2005, Munch and Salinas 2009, Dillon et al. 2010, Marotta et al. 2014). Many suggest that global warming is likely to enhance both primary production and respiration (Smith and Kemp 1995, Caffrey 2003, Allen et al. 2005, Staehr and Sand-Jensen 2006, Davidson and Janssens 2006, Dillon et al. 2010, Marotta et al. 2014).

The positive relationship between temperature and metabolism predicted by the metabolic theory of ecology may be confounded by indirect influences of temperature or its independent covariates. For instance, drought can make ecosystems less productive even as temperatures warm (Zhao and Running 2010). Changes in resource quality can also amplify or dampen the apparent temperature dependence of metabolism (Cross et al. 2015). Changes in community composition (Kratina et al. 2012) and cloud cover (Carbone et al. 2013) have been shown to confound the fundamental relationship between temperature and metabolism. The temperature dependence of aquatic metabolism can be altered by temperature driven changes in the oxygenation or salinity of water (Claireaux and Lagardère 1999, Pörtner and Knust 2007). Thus, while the generalized temperature dependence of metabolism may be fundamental and

consistent across sites, there can be a significant amount of variability in the “apparent” temperature dependence of metabolism due to the indirect influence of temperature or its independent covariates.

Lake Tanganyika is the deepest and oldest lake in the tropics and while it is a nutrient-poor and low-productivity lake, it also supports one of the most species-rich and productive freshwater fisheries in the world (Coulter and Mubamba 1993). Pelagic (offshore) gross primary production has been shown to decrease with temperature even over small temperature ranges (~ 2 °C) on interannual timescales (O’Reilly et al. 2003, Tierney et al. 2010, Loiselle et al. 2014) and seasonal timescales (Plisnier et al. 1999, O’Reilly 2006). The apparent negative temperature dependence of gross primary production seemingly contradicts the prediction from metabolic theory that warming increases metabolic rates (Yvon-Durocher et al. 2012). Lower productivity at higher temperatures in Lake Tanganyika has been explained by climate-change mediated shifts in the strength of water column stratification (O’Reilly et al. 2003, Verburg and Hecky 2009, Tierney et al. 2010). Higher surface temperatures amplify the density stratification of the water column thereby dampening vertical mixing and trapping nutrients below the photic zone (Kraemer et al. 2015). Consequently, pelagic primary productivity in Lake Tanganyika has an “apparent” negative relationship to temperature due to an indirect influence of temperature on lake stratification. Thus, the net effect of diminished nutrient supply due to warming appears to overwhelm the expected boost in potential primary productivity as the water warms, yielding negative “apparent” temperature dependence.

The temperature dependence of consumer metabolism in Lake Tanganyika remains uncertain. This uncertainty stems from the potential for consumers to also have a negative “apparent” temperature dependence arising from lower food availability when the surface of the

lake warms. The strict prediction from the metabolic theory of ecology is that metabolism will increase with temperature at both the ecosystem level (Yvon-Durocher et al. 2012) and the organismal level (Gillooly et al. 2001, Vanni 2002, Savage et al. 2004, Clarke 2004) in proportion to the Boltzmann-Arrhenius factor. If consumer metabolism is tightly constrained by the Boltzmann-Arrhenius factor in Lake Tanganyika, warming may result in metabolic deficits whereby primary production decreases with temperature and the metabolic demands of consumers, increase. But if consumer metabolism is more tightly constrained by endogenous primary productivity, it may also exhibit negative apparent temperature dependence in tandem with primary production. Despite the high likelihood of warming causing metabolic imbalances for consumers in Lake Tanganyika, the temperature dependence of consumer metabolism has not yet been estimated based on field data.

To determine the apparent temperature dependence of metabolism in Lake Tanganyika, we fit Boltzmann-Arrhenius models to organismal and ecosystem metabolism data over the seasonal temperature cycle. Temperature-dependent variables in our analysis fell into two major categories: ecosystem responses (pelagic primary production, pelagic ecosystem respiration, littoral gross primary production, and littoral ecosystem respiration) and fish responses (fish metabolism, and fish excretion rates of two key nutrients: ammonium (NH_4) and soluble reactive phosphorus (SRP)).

We use the relationship between metabolic variables and temperature to determine whether they match what would be predicted from metabolic theory alone. For the ecosystem responses listed above, we use chlorophyll- α specific rates to factor out variability in lake stratification and better estimate the direct effect of temperature alone. Furthermore, we use the directionality of fish metabolic responses and fish body condition responses to temperature to

test whether fish are above or below their apparent temperature optima. Increases in fish metabolism and body condition with temperature would indicate that fish are below their apparent temperature optima whereas decreases in fish metabolism and body condition would indicate that fish are above their apparent temperature optima (Dell et al. 2011). Here we use the term “apparent” temperature optima to indicate that the metabolic optima are not only a function of temperature but also other variables that are correlated to temperature such as food availability. In sum, this analysis will help resolve the potential links between fish, metabolic kinetics and lake hydrodynamics. Resolving these links will provide insights into the impacts of climate warming on the biota of this remarkable tropical lake.

Methods

To estimate the apparent temperature dependence of metabolism in Lake Tanganyika, we fit Boltzmann-Arrhenius models to data over the seasonal temperature cycle. We used Theil-Sen slope estimator, a non-parametric linear model (Theil 1950, Sen 1968, Peng et al. 2008), to estimate ecosystem and organism metabolism as a function of standardized temperature, $1/(kT_c) - 1/(kT)$, where k is the Boltzmann constant ($8.62 \times 10^{-5} \text{ eV K}^{-1}$) T_c is the average temperature over the seasonal temperature cycle ($26.78 \text{ }^\circ\text{C}$), and T is the temperature in Kelvin. Fish body condition was modeled against the average temperature over the month leading up to the measurement because fish body condition is a more time-integrative measure of the conditions affecting fish fitness. Daily estimates of ecosystem fluxes were natural log-transformed prior to model fitting. Fish excretion rates and fish respiration rates were scaled to the average for each species and natural log-transformed prior to model fitting using the equation, $\ln(x/x_s)$, where x is a measurement on an individual from species “s,” and x_s is the average for that species. We calculated Theil-Sen slopes for each response variable pooled across fish species and separately

for each fish species. These slope estimations for fish metabolic responses reflect the sum of direct and indirect temperature effects of temperature on metabolism.

In standard Boltzmann-Arrhenius model fitting, the slope estimates described in the previous paragraph are interpreted as the “activation energy” of the underlying biochemical reactions involved with each specific metabolic rate. Here, we use the term, “apparent activation energy” in recognition that the direct effect of temperature on biochemical reactions underlying metabolism may be confounded by indirect effects. The significance of the apparent activation energy for each response to temperature was assessed using the distribution of all pair-wise slope estimates from the Theil-Sen slope calculations in the “R” package, “mblm” (Theil 1950, Sen 1968, Peng et al. 2008).

Positive activation energies for fish responses to temperature would suggest that fish are below their “apparent temperature optima” and negative slopes would suggest that fish are above their “apparent temperature optima” over the temperature range where data are collected (Dell et al. 2011). We use the word, “apparent” here as well in recognition that estimates of temperature optima based on field data may reflect optima in other environmental variables that are correlated to temperature (like food availability).

Ecosystem fluxes

We measured pelagic gross primary production and ecosystem respiration daily from 20 July, 2012 to 19 September, 2012 and from 29 November, 2012 through 18 April, 2013. We estimated pelagic ecosystem fluxes based on free-water, diel variation in dissolved oxygen at one offshore site (4.903766 °S, 29.590183 °E) approximately 1.5 km from shore near Kigoma, Tanzania. We measured dissolved oxygen every 10 minutes at a depth of 15m below the surface

using an optical dissolved oxygen probe on an YSI 6600 sonde. The sonde also measured specific conductivity and temperature and was deployed on a subsurface mooring. At this location, the depth of the water column is 140 m and the thermocline typically ranges from 40-70 m depth. Thus, the dissolved oxygen sensor was well above the thermocline within the photic zone of the lake.

We also measured littoral gross primary production and ecosystem respiration at a rocky nearshore site (4.913400 °S, 29.598350 °E) at Jacobsen's beach near Kigoma, Tanzania continuously from 19 July, 2012 to 14 August, 2013. We used an YSI 6600 sonde to measure water temperature and dissolved oxygen at 5 meters depth with the dissolved oxygen sensor 15 cm above the rocky bottom. The deployment at 5 meters depth is above the thermocline, within the photic zone of the lake, and below the average depth to which wave surges penetrate (generally 2-4 m). The sensor was located 15 meters from shore. The variation in dissolved oxygen at this location is assumed to primarily reflect benthic primary production and respiration due to the proximity of the sensor to the benthos.

To estimate daily gross primary production and ecosystem respiration at the pelagic and littoral site, we used a state-space model with maximum likelihood estimation and a Kalman filter (Read et al. 2011, Batt 2012, Winslow et al. 2015). We estimated the gas transfer coefficient daily using wind speed data from a nearby land-based weather station (Cole and Caraco 1998, Staehr et al. 2010).

We assessed whether the fundamental, direct temperature dependence of ecosystem metabolic rates differed from that predicted from the metabolic theory of ecology. To disentangle the direct and indirect effects of temperature, we calculated chlorophyll- α specific ecosystem metabolism rates over the seasonal temperature cycle. Chlorophyll- α was measured using an

optical chlorophyll- α sensor which was calibrated to chlorophyll- α extractions measured using an Aquafluor brand, handheld fluorometer. We expected chlorophyll- α specific metabolic rates to more closely match the temperature dependence of metabolism predicted from metabolic ecology because they control for the effects of producer mass in the ecosystem (López-Urrutia and Morán 2007, Yvon-Durocher et al. 2010).

Consumer metabolism

We measured fish body condition and excretion rates on 6 species of littoral fishes (*Lepidolamprologus elongatus* (n=55), *Neolamprologus brichardi* (n=55), *Neolamprologus mondabu* (n=56), *Ophthalmotilapia heterodonta* (n=52), *Petrochromis kasumbe* (n=72), and *Tropheus brichardi* (n=70)) over the seasonal temperature cycle. These species were chosen to represent the most abundant species of fish from five of the main trophic groups in the littoral fish community: benthic algivores, benthic invertivores, planktivores, omnivores, and piscivores. 5-7 individual fish from each species were captured near the littoral sonde deployment every 1.5 months from June 2012 to August 2013, totaling 360 fish. Individual fish were targeted to represent a size range that closely reflected the size range of fish in the rocky littoral habitat from which they were caught.

Ammonium (NH_4) and soluble reactive phosphorus (SRP) excretion rates were measured by incubating fish in 1-2 gallon Ziploc bags filled with 2 or 3 L of filtered lake water depending on the size of the fish. After fish were caught, they were immediately placed into an incubation bag which was partially submerged in the lake to maintain temperatures that matched lake temperatures. NH_4 samples were taken before and after 30 minute incubations and analyzed with a handheld fluorometer within 24 hours of being collected. We calculated NH_4 concentrations while accounting for matrix effects and background fluorescence using an unamended sample

and three spiked samples (Taylor et al. 2007). SRP samples were also taken before and after the fish incubations and kept frozen during transport to UW-Madison where they were analyzed using the standard molybdate blue method on an autoanalyzer. Excretion rates were determined by subtracting the initial mass of NH_4 and SRP from the final mass after the incubation and dividing by the incubation time.

The live weight, standard length, and total length of each fish was measured and used to estimate species-specific mass scaling exponents for length and excretion rates. We estimated the body condition of each fish using the Weight/Length^{*n*} ratio where *n* is the species-specific mass-length scaling coefficient estimated from the entire data set. This is a standard metric for fish body condition widely used when more detailed information is not available (Bolger and Connolly 1989).

Fish respiration rates were measured over a portion of the seasonal temperature cycle from June-August 2012 and from July-August 2013. Closed system respirometry (Steffensen 1989, Urbina et al. 2012) was used to measure metabolism in seven species of littoral fish (*Lepidolamprologus elongatus* (*n* = 14), *Lamprologus lemarii* (*n* = 13), *Eretmodus cyanostictus* (*n* = 15), *Tropheus brichardi* (*n* = 100), *Neolamprologus brichardi* (*n* = 15), *Altalamprologus compressiceps* (*n* = 15), and *Perissodus microlepis* (*n* = 13)). Two respirometry chambers (61 cm long and 700mL volume) were constructed from PVC with caps on both ends and a rubber sealed port on the top. Fish were caught from one of eight rocky littoral sites along a 20 km stretch of shoreline north and south of Kigoma, Tanzania. After being caught, individual fish were immediately placed into a respirometer with a dissolved oxygen probe inserted into the rubber sealed port. Each fish was allowed to acclimate to the respirometer for 30 minutes. Changes in dissolved oxygen over 20-40 minute incubations were compared to changes in the

control chamber without a fish. We also kept 85 individual *Tropheus brichardi* for 12 hours in plastic buckets without food to allow them to clear their guts. Respiration rates on these semi-starved fish were measured at the end of the 12-hour waiting period using the same methods.

Results

Direct temperature dependence of ecosystem metabolism

When we used chlorophyll-a specific ecosystem metabolism rates to factor out the influence of the indirect effects of temperature on metabolism, the temperature dependence of ecosystem carbon cycling was within the range for that predicted from metabolic theory (Fig 1). The activation energy for littoral gross primary production (1.29 ± 1.02 eV, $p = 0.01$) was not significantly different from what has been shown for aquatic ecosystems (0.35 eV) (Yvon-Durocher et al. 2010, 2011). The activation energy for littoral ecosystem respiration (1.68 ± 0.99 eV, $p < 0.01$) was slightly higher than what has been predicted from mesocosm studies (0.62 eV) (Yvon-Durocher et al. 2010) and meta-analyses (0.55 eV) (Yvon-Durocher et al. 2012) but well within the range of activation energies reported for other freshwater metabolic rates (Dell et al. 2011). Both of these estimates of fundamental activation energies was significantly different from zero ($p > 0.1$). The activation energies for chlorophyll-specific pelagic gross primary production and pelagic ecosystem respiration (0.50 ± 1.39 eV and 1.37 ± 1.80 eV, respectively) were also not significantly different from that predicted from metabolic ecology (0.35 eV) (Yvon-Durocher et al. 2012).

Apparent temperature dependence of ecosystem metabolism

The apparent temperature dependence of ecosystem metabolism diverged from the chlorophyll- α specific activation energies (Fig. 2 and Fig. 3). Pelagic gross primary production

was negatively related to temperature ($E_a = -3.96 \pm 0.82$ eV). Littoral gross primary production is also negatively related to temperature but with a lower activation energy (-2.05 ± 0.51 eV). Ecosystem respiration rates were highly correlated to ecosystem gross primary production in both the littoral and pelagic zones. Apparent activation energies for pelagic and littoral ecosystem respiration were -4.89 ± 1.01 eV and -1.88 ± 0.58 eV, respectively. None of the four ecosystem fluxes had apparent activation energies that agreed with the fundamental prediction from the metabolic theory of ecology.

Apparent temperature dependence of consumer metabolism

Consumer metabolism was negatively related to temperature for five out of ten species in at least one of the three metabolic responses measured here (Fig. 3). The species that observed negative apparent temperature dependence for at least one of the metabolic variables measured here were *Lepidolamprologus elongatus*, *Lamprologus lemarii*, *Tropheus brichardi*, *Ophthalmotilapia heterodonta*, and *Neolamprologus mondabu*. The negative activation energies reported for these species are outside the range of freshwater metabolic responses for organisms that are within their optimal range (0.005 – 2.56 eV) (Dell et al. 2011).

The apparent fish respiration responses to temperature varied considerably across species (Fig. 3). Three of the fish species analyzed here (*Lepidolamprologus elongatus*, *Lamprologus lemarii*, and *Eretmodus cyanostictus*) exhibited metabolic falls with apparent activation energies ranging from -0.38 to -1.48 eV. Four species had respiration rates that increased with temperature (*Tropheus brichardi*, *Neolamprologus brichardi*, *Altolamprologus compressiceps*, and *Perissodus* sp.) with apparent activation energies ranging from 0.03 to 1.97 eV (Fig. 3).

The temperature dependence of excretion rates were also highly variable across fish species (Fig. 3). Five out of six species had NH_4 excretion rates that were negatively related to temperature with apparent activation energies ranging from -0.39 to -1.35. Four of these negative responses to temperature were significantly different from zero ($p < 0.05$) and all of them were significantly different from the predicted activation energy for excretion rates based on metabolic theory (Vanni 2002). *Petrochromis kasumbe* had a significant positive apparent activation energy ($E_a = 2.39 \pm 1.46 \text{ eV}$, $p < 0.01$) that was within the range of common freshwater activation energies (Dell et al. 2011). NH_4 excretion activation energies were highly correlated to average, mass-scaled NH_4 excretion rates across species. SRP excretion apparent activation energies ranged from -2.49 to 2.30 with three out of six being significantly different from zero and significantly different from the prediction based on metabolic ecology (Vanni 2002) ($p < 0.01$). SRP excretion rate activation energies were not correlated to the average mass-scaled SRP excretion rate across species ($p > 0.05$).

The body condition of all six species of fish declined with temperature, three of which were significant (*Lepidiolamprologus elongatus*, *Tropheus brichardi*, and *Neolamprologus brichardi*, $p < 0.05$) (Fig. 4). The declines in body condition with temperature observed here correspond to a 2-11% reduction in body condition per 1 °C of warming. Slopes for fish body condition were negatively correlated ($r = -0.91$) to the apparent activation energy for SRP excretion rates across fish species but not to the apparent activation energy for NH_4 excretion rates. There was an overall inverse relationship between loss of body mass and SRP excretion across species. The species with the largest seasonal declines in body condition had the largest increases in SRP excretion with temperature. Fish with smaller declines in body condition had low or negative activation energies for SRP excretion rates.

Discussion

The metabolic theory of ecology predicts that metabolic rates at the organism and ecosystem scale will increase with temperature. The direct temperature dependence of ecosystem metabolism estimate here roughly matches this prediction. However, our results on the “apparent” temperature dependence of metabolism in Lake Tanganyika demonstrate a stark departure from this prediction. All aspects of whole-ecosystem metabolism analyzed here (littoral gross primary production, littoral ecosystem respiration, pelagic gross primary production, and pelagic ecosystem respiration) respond negatively to temperature suggesting that warming-induced changes in lake stratification belie the fundamental temperature dependence of metabolism. Some aspects of fish metabolism and fish body condition analyzed here also decrease significantly with temperature, suggesting that some fish are already above their “apparent” thermal optima.

Ecosystem responses to temperature

It is well established that pelagic primary production in Lake Tanganyika is negatively related to surface temperature based on sediment core data (O’Reilly et al. 2003, Tierney et al. 2010), in situ observations (Plisnier et al. 1999, Plisnier 2001), and remote sensing data (Loiselle et al. 2014). This substantial decline in pelagic productivity has been demonstrated over small temperature ranges (~ 2 °C) similar to the temperature range in our analyses. We corroborate these findings with pelagic gross primary production estimates based on free water dissolved oxygen data. Our results closely match inferences from remote sensing data which has shown $\sim 40\%$ reductions in pelagic gross primary productivity in the warm season near our study site over the entire seasonal temperature and wind cycle (Bergamino et al. 2010). Such massive

reductions in primary productivity over such small temperature ranges (~ 2 °C) demonstrates the extraordinary sensitivity of Lake Tanganyika to temperature variation and lake stratification.

Littoral gross primary productivity is also negatively related to temperature on seasonal timescales at our study site. Littoral gross primary production was less sensitive to temperature than pelagic gross primary production (apparent activation energy closer to zero) suggesting that the cumulative direct and indirect effects of temperature on littoral productivity may be dampened relative to the pelagic zone. Several characteristics of littoral ecosystems may explain the dampened apparent temperature dependence there. Tight nutrient recycling between fish and benthic algae may serve to reduce nutrient losses from littoral ecosystems thereby maintaining higher productivity through periods of low nutrient supply. Nutrient runoff from terrestrial ecosystems may also help support littoral primary production in the warm season more so than pelagic primary production. While nutrient runoff is generally thought to only be a marginal component of the lake's annual nutrient budget, it may be an important source of localized nutrients to nearshore areas in the warm season when vertical mixing is reduced (Langenberg et al. 2003). Tight nutrient recycling and nutrient runoff may serve to dampen the apparent negative temperature dependence of littoral gross primary production. However, even with those sources of nutrients, the negative apparent relationships between littoral gross primary productivity and temperature diverge strongly from what would be predicted from metabolic theory alone.

Ecosystem respiration in both the pelagic and littoral zones were also negatively related to temperature and highly coupled to primary productivity in their respective lake zones. The activation energies for pelagic and littoral ecosystem respiration were well outside the range reported by a recent global meta-analysis (Yvon-Durocher et al. 2012), although tropical lakes were underrepresented in the meta-analysis and most lakes had data over a wider seasonal range

in temperature. The negative apparent activation energies for ecosystem respiration suggests that in Lake Tanganyika, ecosystem respiration is more tightly constrained by endogenous gross primary production than by temperature. The relative dearth of imported exogenous primary production at our field sites may restrict the temperature dependence of ecosystem respiration, forcing it to match the temperature dependence of primary production. In other lakes where exogenous carbon sources make up a substantial component of the ecosystem carbon demand, ecosystem respiration may be decoupled from endogenous gross primary production. With ample exogenous carbon inputs, the temperature dependence of ecosystem respiration would be expected to more closely resemble the temperature dependence predicted from metabolic theory. The relatively strong negative relationship between temperature and ecosystem respiration in the pelagic zone (apparent activation energy: -4.89 ± 1.01 eV) may reflect the scarcity of alternate carbon sources when endogenous primary productivity declines.

The apparent activation energies we report reflect the sum of all indirect influences and the direct influence of temperature on metabolism. We were able to distinguish between the direct, kinetic influence of temperature and the indirect influences of warming-induced shifts in lake stratification (Fig 1 and Fig 2). This suggests that the underlying fundamental dependence of littoral gross primary production and littoral ecosystem respiration on temperature via chemical kinetics may still closely match that predicted from metabolic theory.

Fish responses to temperature

The direct and indirect influence of temperature on fish was a primary concern in our study because fish from the littoral zone of Lake Tanganyika make up a substantial component of littoral ecosystem biomass (McIntyre et al. 2007), are a critical source of protein for adjacent human populations (Coulter and Mubamba 1993), represent a globally significant repository of

vertebrate biodiversity (Vadeboncoeur et al 2011), and are subject to a host of anthropogenic stressors (Cohen et al. 1993, Alin et al. 2002, Manirakiza et al. 2002, Donohue et al. 2003).

The temperature dependence of fish metabolism (respiration, NH_4 excretion, and SRP excretion) was highly variable across species. This variability may be due in part to seasonal variation in food availability and the proximity of some fish to their thermal optima. For most of the fish species in our analysis (five of seven), the apparent activation energy for fish respiration was statistically indistinguishable from the fundamental temperature dependence of fish metabolism estimated from meta-analyses (Gillooly et al. 2001). Thus, the metabolic demands of these fish are likely to increase with temperature even as gross primary production and food availability goes down. Increased food demands in the face of decreased food supply suggests that at higher temperature, fish will have less discretionary energy for growth and reproduction. The resulting metabolic deficit may be especially problematic for Lake Tanganyika's algivorous fish that depend directly on benthic primary production.

Two species of fish (*Lepidolamprologus elongatus*, *Lamprologus lemarii*, both primarily piscivorous) exhibited negative activation energies for fish respiration. Their negative apparent activation energies were significantly below the prediction for fish living within their optimal temperature range, suggesting that they are above their apparent thermal optima for at least some of the year. The activation energies for respiration in these two fish species together with the metabolic rates of semi-starving *Tropheus brichardi* were not significantly different from the fundamental temperature dependence of catabolism estimated by a recent meta-analysis (-1.15 ± 0.39 eV) (Dell et al. 2011). This suggests that like the semi-starving *Tropheus brichardi*, *Lepidolamprologus elongatus* and *Lamprologus lemarii* may also not get enough food to meet

their metabolic demands at higher temperatures, leading to decreased performance (Rummer et al. 2014).

Variation in NH_4 excretion rates across species also likely reflect differences in the seasonality of food availability. NH_4 excretion tended to significantly decrease with temperature across most species in our incubations. Underfed fish tend to have lower NH_4 excretion rates than fed fish (Buttle et al. 1995, Whiles et al. 2009), thus seasonal availability of food resources could underlie the negative temperature dependence of most fish species' NH_4 excretion rates. Fish species that excrete the most NH_4 per unit biomass had the most positive apparent activation energy for NH_4 excretion rates ($r=0.84$). *Petrochromis kasumbe*, a common benthic algivore that inhabits the rocky nearshore zone of Lake Tanganyika, had a strong increase in NH_4 excretion rates with temperature which may reflect its diet. Unlike many aquatic benthic herbivores in lake Tanganyika that specialize on eating filamentous algae, *Petrochromis* species have rasping mouthparts for scraping biofilms off rocks (Kassam et al. 2003). Thus, their diet not only consist of diatoms and filamentous algae but also cyanobacteria and unicellular algae that live deeper within the biofilm and are richer in nitrogen. In addition to having the highest apparent activation energy for NH_4 excretion rates, *Petrochromis kasumbe* also had the highest mass-scaled excretion rate of any fish that we incubated.

All six species of fish in our study had decreased body condition at higher temperature, four of which were at least marginally significant ($p < 0.1$). The species of fish with the largest decline in body condition was *Lepidiolamprologus elongatus*, a common piscivore that is likely above its apparent temperature optimum. The species with the smallest decline in body condition was *Ophthalmotilapia heterodonta*; an omnivore that may have the greatest capacity to switch its diet between algae and other food sources when endogenous primary production decreases.

The relationship between fish body condition and temperature was highly correlated to the apparent activation energy for SRP excretion across species. The four species with the largest declines in body condition all had positive activation energies for SRP excretion rates. The two species with negative apparent activation energies for SRP excretion had the smallest decreases in body condition. This observation suggests that fish above their apparent temperature optima excrete more SRP than fish below their apparent temperature optima. From this pattern, we infer that as fish become temperature stressed or food limited in the warm season, they may catabolize their own proteins and nucleic acids or have less need to retain dietary phosphorus for growth and reproduction. The increase in Catabolism and decreased need for phosphorus at higher temperature would lead to higher SRP excretion rates in the warm season. Reductions in body condition may also involve partial clearance of bone mass (Huusko et al. 2011, Bendik and Gluesenkamp 2013) which would be a potent source of excreted SRP.

Reductions in fish body condition with temperature reported here may reflect losses in either somatic or reproductive tissue mass. Seasonal variability in reproduction and gonadal tissue mass have not been thoroughly explored in Lake Tanganyika, but, many species of Tanganyikan cichlids have demonstrated a capacity to reproduce year-round in aquaria when resources are abundant. Work from other East African Great Lakes suggests that when nutrients are limiting, fish reproduce year-round with moderate seasonal peaks coinciding with high food availability (Witte 1980, Marsh et al. 1986, Gordon and Bills 1999). Thus the seasonal variability in body condition may reflect seasonal variability in gonadal mass as opposed to warming-induced catabolism of fats and proteins. Thus, in Lake Tanganyika, decreases in food availability as a result of surface warming may reduce discretionary energy for reproduction. Whether the decrease in body condition we observed reflected losses of somatic or gonadal tissues, the

implications of warming for fish fitness remain grim. However, in the unlikely scenario that seasonality in gonadal mass arises from a seasonal pattern unrelated to food availability, gonadal tissues may still be unaffected by long-term warming.

Climate warming implications

Using the apparent temperature dependence of metabolism fit to data over seasonal timescales to infer climate warming impacts assumes that the interannual temperature dependence of metabolism will closely match seasonal temperature dependence. This assumption may be reasonable given that the mechanism which directly links temperature to metabolism (chemical kinetics) is likely to function similarly over seasonal and interannual scales (Yvon-Durocher et al. 2012). Furthermore, temperature and hydrodynamic variables are correlated on seasonal and interannual timescales (Supplementary Figure S1), thus, the primary mechanism which indirectly links temperature to metabolism (wind and lake hydrodynamics) is also likely to function similarly over seasonal and interannual timescales. However, there are some potential drivers of metabolism that are correlated to temperature only on seasonal timescales or only on interannual timescales. These differences could affect the climate change implications of our study. For instance, the carbon dioxide concentration in the atmosphere did not vary substantially over the duration of our study but is positively correlated to temperature on interannual timescales. A long-term increase in dissolved carbon dioxide concentrations in Lake Tanganyika could have a fertilizing effect on lake primary production (Jansson et al. 2012) that could partially offset the reduction in primary production resulting from changes in lake stratification. Nevertheless, our results suggest that 1 °C of seasonal warming would lead to roughly a 20% reduction in pelagic gross primary production. This matches the approximate reduction in gross primary production estimated from other work on seasonal variation in pelagic

primary production (Bergamino et al. 2010) and a recent study of the long-term reduction in pelagic primary production resulting from climate change (O'Reilly et al. 2003). Thus, seasonal responses to temperature may be a reasonable first approximation of interannual responses to climate warming.

As climate change warms Lake Tanganyika, chronic seasonal reductions in fish body condition (Weight/Lengthⁿ) may result in absolute reductions in fish size over time (weight, length, etc.). Shrinking body size is a known consequence of climate change induced shifts in metabolism and environmental variables (Todd et al. 2008, Daufresne et al. 2009, Cheung et al. 2012). Size reductions as a result of climate warming have been observed in a wide variety of taxa including plants, insects, birds, mammals, and fish (Daufresne et al. 2009). Reductions in body condition and body size in the fish of Lake Tanganyika would have implications for the hundreds of thousands of people who depend on these fish as their primary source of protein.

The evidence presented in this paper for wide-ranging effects of warming on ecosystem and organismal metabolism in Lake Tanganyika raises the possibility that other lakes may be experiencing similar impacts of climate change. We suspect that warm oligotrophic lakes where most of the nutrient demand is met by vertical mixing are most likely to have negative apparent activation energies for gross primary production. Correlations between temperature and photo-inhibition or ultra-violet light exposure, cloud cover, and wind speed might also give rise to negative apparent temperature dependencies. In fact, many tropical or low elevation lakes have been shown to exhibit negative correlations between temperature and primary productivity including Lake Kyoga (Loiselle et al. 2014), Lake Kivu (Loiselle et al. 2014, Darchambeau et al. 2014), Lake Carioca (Brighenti et al. 2015), Lake Dom Helvecio (Brighenti et al. 2015), Lake Titicaca (Richerson et al. 1986), Lake Nkuruba (Saulnier-Talbot et al. 2014), Pink Lake

(Hammer 1981), Lake Kariba (Regina 2012, Ndebele-Murisa et al. 2014), Lake Rotorua (Yvon-Durocher et al. 2012), Lake Toreadora (Michelutti et al. 2015), and Lake Chorerras (Michelutti et al. 2015). Whether these lakes are idiosyncratic or part of a systematic response to temperature across the tropics remains uncertain. We recommend further investigation into the mechanisms leading to metabolic decreases in lakes as a response to warming. There is a strong need to integrate this pattern into our predictions of lake responses to climate warming as they contradict those predicted by metabolic theory alone.

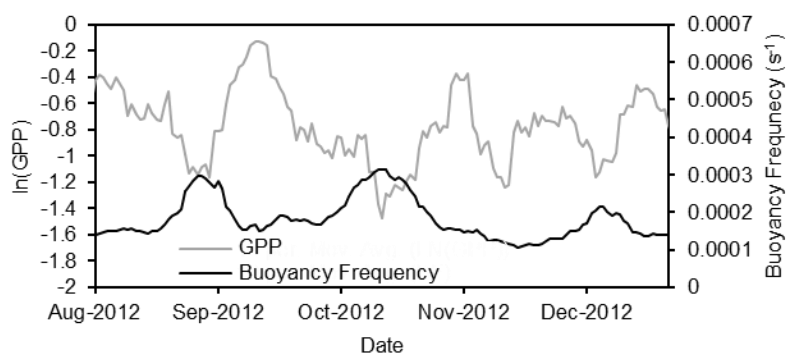
Acknowledgements

We are grateful for field research funding from the National Science Foundation (NSF) (DEB-1030242 and DEB-0842253). This work was also supported by the University of Wisconsin-Madison. Weather station data were contributed to this effort by the Tanzania Fisheries Research Institute-Kigoma and the Nanjing Institute of Geography and Limnology, Chinese Academy of Sciences. Research clearance was provided by the Vice Chancellor of the University of Dar es Salaam, Tanzania. Thanks to Rashid Tamatamah and Mupape Mukuli for their assistance navigating the immigration and research clearance processes. Thanks to dive expert and fish specialist, George Kazumbe for his help identifying and capturing fish in the field.

Supplementary Materials

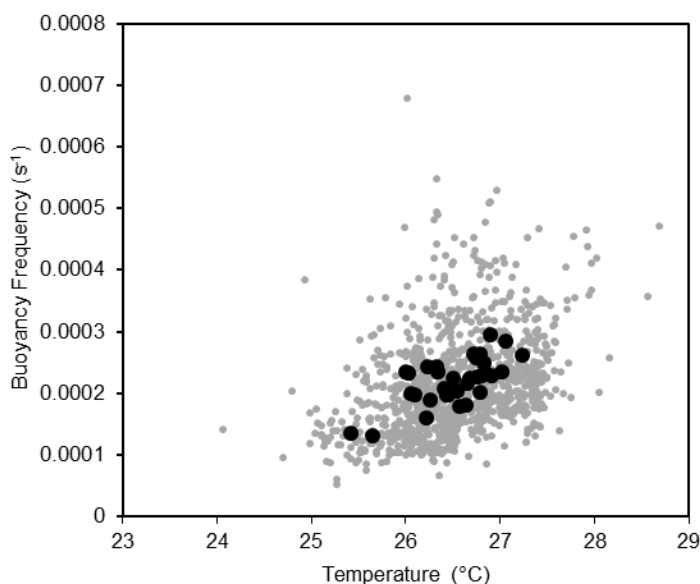
Supplementary Figure S1: Time series of littoral gross primary production (GPP) and thermocline buoyancy frequency from August to December, 2012 at a site in Lake Tanganyika near Kigoma, Tanzania. Thermocline buoyancy frequency is an estimate of the strength of the thermocline and is linked to the level of vertical mixing in the water column. Peaks in thermocline strength coincide with decreases in littoral gross primary production. Lake

temperature profiles were measured on the offshore mooring to which the pelagic sonde was attached every 10 minutes from 20 July, 2012 to 19 September, 2012 and from 29 November, 2012 through 18 April, 2013. Temperature was measured at 10, 20, 30, 40, 50, 55, 60, 70, 80, 90, and 120 m depths. We supplemented these discrete temperature profiles with a weekly temperature profile cast with temperature measured every 0.1 meters and interpolated to a daily time step. Temperature profiles were used to calculate three lake mixing indexes: thermocline depth and buoyancy frequency. The thermocline depth is the depth of the maximum density change with depth in the water column and is a key variable controlling the depth distribution of solutes [Weyhenmeyer et al., 2011]. The Brunt-Väisälä buoyancy frequency (hereafter “buoyancy frequency”) is the angular frequency at which a parcel of water would oscillate if it was displaced from its location in the water column. We calculated the buoyancy frequency at the thermocline for each temperature profile to estimate the steepness of the thermocline—a key control on vertical mixing in aquatic systems [Wüest and Lorke, 2010]. High-buoyancy frequency signifies that the thermocline is steep and the resistance to vertical mixing at the thermocline is pronounced.



Supplementary Figure S2: Thermocline buoyancy frequency as a function of lake surface temperatures. Data are from lake temperature data collected discontinuously since 1912 in Lake

Tanganyika (Kraemer et al. 2015). Grey dots represent temperature and buoyancy frequency estimates from individual temperature profiles. Large, black dots represent annual averages. We also used a century of temperature profiles from around the northern basin of the lake (Kraemer et al. 2015) to determine whether temperature and buoyancy frequency were correlated on seasonal and interannual timescales. Buoyancy frequency and thermocline depth were calculated using the package, “LakeAnalyzer” in R (Read et al. 2011, R Development Core Team 2013). Thermocline buoyancy frequency, a key control on lake productivity, was highly correlated to surface temperature on daily ($r = 0.37$) and interannual ($r = 0.68$) timescales. Thermocline depth, another important control on lake productivity was also correlated to surface temperature on daily ($r = -0.18$) and interannual ($r = -0.51$) timescales.



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Figures

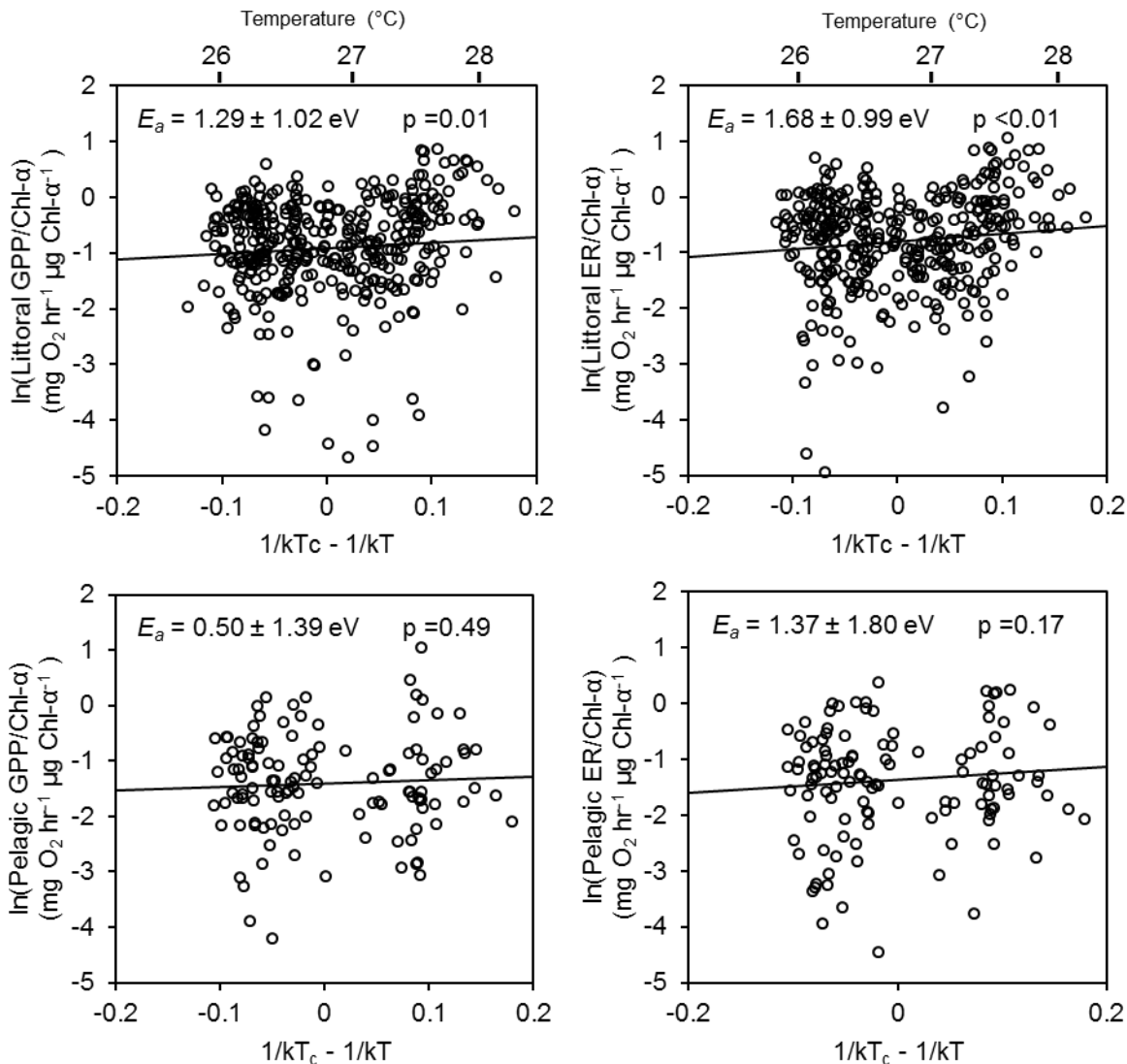


Figure 1: Arrhenius plots showing the relationship between the natural logarithm of each chlorophyll- α specific metabolic rate against the standardized temperature $(1/kT_c) - (1/kT)$ where k is the Boltzmann constant (8.62×10^{-5} eV K⁻¹), T_c is the average temperature over the seasonal temperature cycle (299.93 °K), and T is the temperature in Kelvin. The equivalent temperature in °C is also reported on the top panels in the figure. Littoral and pelagic ecosystem respiration (ER) and gross primary production (GPP) were calculated based on free water dissolved oxygen

data at sites near Kigoma, Tanzania. Temperature values are standardized to the mean temperature across all measurements for the purposes of visualization only.

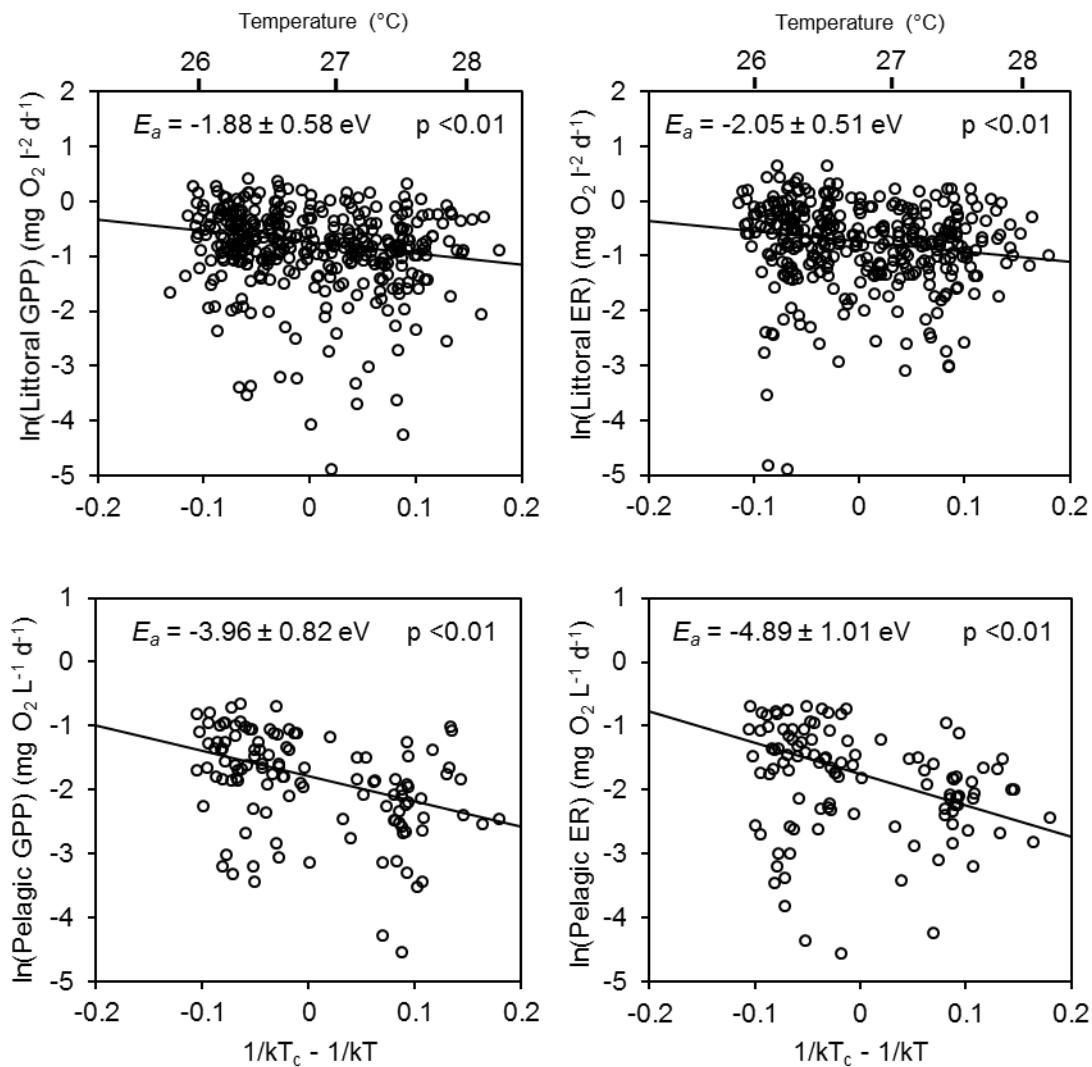


Figure 2: Arrhenius plots showing the apparent relationship between the natural logarithm of each variable against the standardized temperature. Abbreviations as in Fig. 1.

Ecosystem Fluxes

Pelagic Respiration (134)
 Pelagic Gross Primary Production (134)
 Littoral Gross Primary production (384)
 Littoral Respiration (384)

Fish Respiration

Tropheus brichardi (starved) (85)
Lepidolamprologus elongatus (14)
Lamprologus lemairii (13)
Eretmodus cyanostictus (15)
Tropheus brichardi (100)
Neolamprologus brichardi (15)
Altolamprologus compressiceps (15)
Perissodus microlepis (13)

NH₄ Excretion

Tropheus brichardi (70)
Lepidolamprologus elongatus (55)
Ophthalmotilapia heterodonta (52)
Neolamprologus mondabu (56)
Neolamprologus brichardi (55)
Petrochromis kasumbe (72)

SRP Excretion

Ophthalmotilapia heterodonta (52)
Neolamprologus mondabu (56)
Tropheus brichardi (70)
Neolamprologus brichardi (55)
Petrochromis kasumbe (72)
Lepidolamprologus elongatus (55)

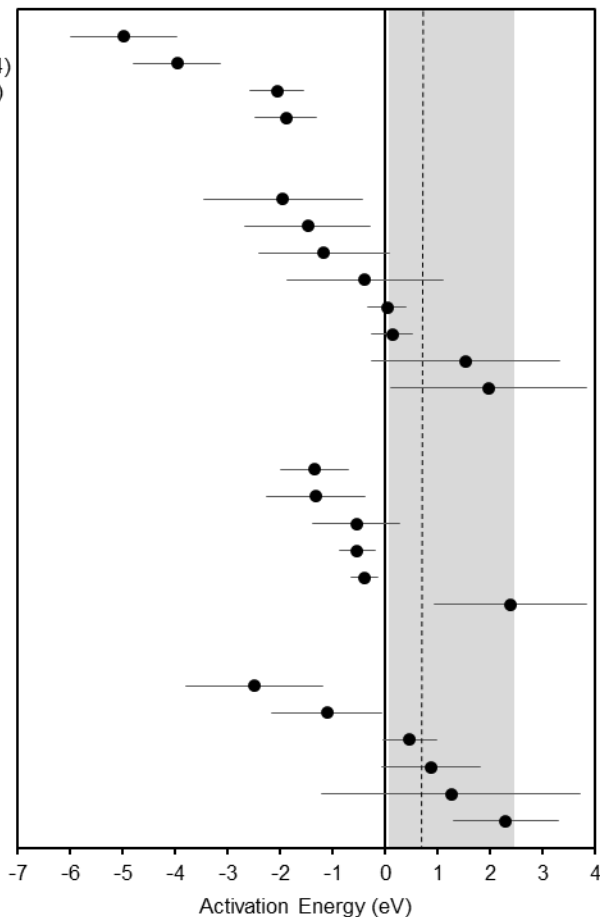


Figure 3: Apparent activation energies and 95% confidence intervals for metabolic responses to temperature in Lake Tanganyika (filled black circles). Activation energies are calculated from the Boltzmann-Arrhenius model based on field data. Responses are grouped by variable and separated out by species or ecosystem flux. Sample sizes are reported in parentheses next to each variable. The vertical dashed line and grey box represent the mean and range for the diversity of fundamental activation energies predicted from metabolic theory.

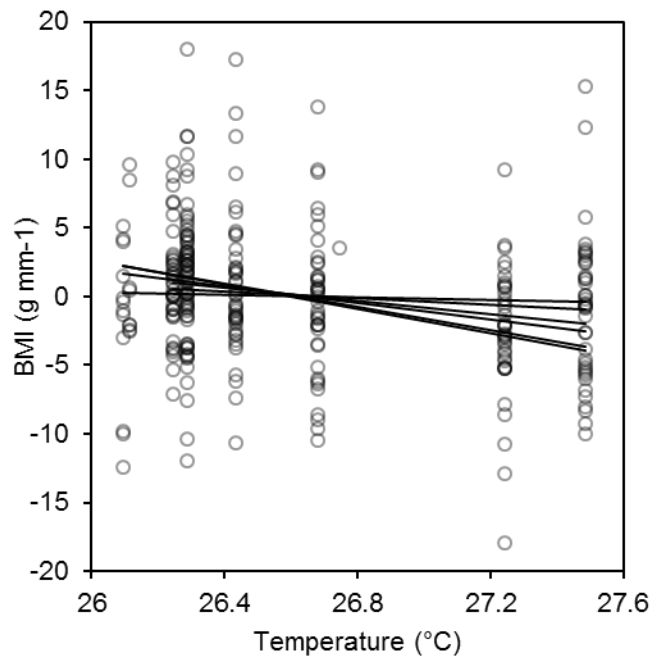


Figure 4: Body mass index (BMI) pooled across six fish species and scaled to be independent of fish mass and fish species. Solid lines represent the Theil-Sen's slope for each of the six species represented in the plot.