Ecological effects of long-term warming in the world's largest lake – Lake Baikal, Siberia

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Throughout the world scientists, policy makers and managers discuss the need for long-term monitoring of ecosystems – to better understand the impacts of management decisions, natural dynamics of ecosystems, or to ensure that human impacts do not surpass some threshold of disturbance to systems of concern (Kremen et al 1993). Even so, managers are well aware that when a budget needs to be tightened, monitoring plans are frequently most vulnerable to excision. Monitoring does not yield exciting results quickly, and may ultimately tell us things about our management that will be uncomfortable to hear. While Westerners hedge about devoting resources to monitoring, in institutions that are politically stable and lavishly funded by international standards (Dezhina & Graham 2005), three generations of one Siberian family have quietly maintained perhaps the world's most astonishing limnological monitoring program on a lake of international renown, Lake Baikal. Surviving the scientific oppression of Stalin (Graham 1993) as well as the political upheaval, dramatic infrastructure reorganization and lack of scientific funding accompanying the fall of the Soviet Union, 60 years of monitoring data from Lake Baikal now provide a window on large-scale ecosystem response to some other human disturbances that have characterized this past century.

Spanning more than 4 degrees of latitude and obtaining a maximum depth greater than 1.6 km, Siberia's Lake Baikal is the world's deepest and most ancient lake; because of its tremendous size, it plays no small part in controlling climate in a region that is experiencing dramatic environmental warming (Serreze et al 2000, Shimaraev et al 2002). Biological diversity of this ancient lake is extraordinary, strongly influencing UNESCO's 1996 decision to designate Lake Baikal a World Heritage Site. Many of these species are endemic – specially evolved to Lake Baikal's environment, a comparatively cold and extreme lake. The unusual endemic fauna include the world's only freshwater pinniped (the Baikal seal *Phoca sibirica*), 344 species of amphipods, and 33 species of sculpin fishes, including the deep-dwelling translucent golomyanka

(*Comephorus baicalensis* and *C. dybowskii*). Some endemic fishes such as the golomyanka strongly resemble the abyssal marine fishes, although their closest relatives are from freshwater.

The Lake Baikal data set, all but completely unknown to the international scientific community until recent years (Hampton et al 2008, Moore et al 2009, Katz et al 2011), is of inestimable scientific importance, spanning 60 years of ecological change at high temporal and taxonomic resolution. Intrigued by seasonal and interannual changes in abundance of lake organisms, Mikhail Kozhov, a professor and director of Irkutsk State University's Biological Institute, began collecting limnological data in 1945 at roughly biweekly intervals. Kozhov's daughter (O.M. Kozhova) and granddaughter (co-author L. Izmest'eva) also attained directorships at Irkutsk State University, and carried on the family legacy of monitoring Lake Baikal.

Since 1945 data have been collected at least monthly in depth profiles from the surface to 250 m at a single main station, approximately 2.7 km offshore from Bol'shie Koty (105°045'02" E, 51°542'48" N). Sixty nine other stations throughout Lake Baikal are surveyed once a year. Treacherously thin ice prohibits collection in some months, generally January. Temperature and Secchi depth (water clarity) are standard measures, and phytoplankton and zooplankton samples are enumerated at the species level and additionally by age class for zooplankton. Phytoplankton (algae) and zooplankton are the microscopic "plants" and animals, respectively, that form the base of the food web in lakes. In addition, chlorophyll a has been measured since 1979, as a proxy for phytoplankton biomass. The Lake Baikal data reveals significant changes occurring in temperature and biomass of phytoplankton, consistent with recent reports of rapid Siberian warming and long-term changes in Lake Baikal's ice cover (Magnuson et al 2000). Concurrently, changes in zooplankton abundance and composition have implications for nutrient cycling in this low-nutrient ecosystem. These long-term trends occur against the backdrop of shorter term climate variability associated with jet stream dynamics, also discernible in the Baikal data.

General Approach to Data Assembly

We used Discrete Short-Time Fourier Transform (DSTFT) on overlapping 10-yr segments of the 60-yr time series, to characterize seasonality that then could be differentiated from long-term trends. Following the DSTFT we assembled two types of data sets:

1) Continuous 60-yr "de-seasoned" time series, with which to explore long-term trends in temperature and plankton abundance. De-seasoning of the time series data successfully removed significant first-order autocorrelation in the residuals in all time series except that of the relatively long-lived copepods, an abundant microscopic grazer with an unusually long lifespan (~2 yr), such that simple linear regression was generally useful for discerning long-term trends.

2) Time series of the attributes that describe the shorter term patterns in the data, e.g. phase (Φ), which can help to describe seasonality (Stine et al 2009, Katz et al 2011). Phase essentially tells us whether seasons begin earlier or later each year relative to other years in the data set. We examined the timing of the seasons, Φ, in relation to large-scale climate patterns by performing cross-correlations with climate indices, to better understand long-term dynamics of temperature in the lake and its watershed.

Long-term Lake Baikal Warming and its Effects

The ice-free season in Lake Baikal is known to have lengthened by 16.1 days over the past 137 years (Magnuson et al 2000), with lake ice (Livingstone 1999) and regional snow (Ye 2001) trends significantly correlated with the North Atlantic Oscillation (NAO) index. Air temperature in the Baikal area has increased over the past century at twice the average global rate (Shimaraev et al 2002). The Baikal data set reveals corresponding changes within the lake.

Water surface temperature has increased over the past 60 yr (Hampton et al 2008) at a rate that is twice that of the increase in average air temperature at the lake (1.2 °C over the past century; Shimaraev et al 2002). This rapid warming is likely related strongly to recession of the winter ice, as has been recognized on Lake Superior in North America (Austin and Colman 2008). While chlorophyll a has increased rapidly over the past quarter century, which ultimately should affect water clarity, this increase in algal biomass has not yet caused a significant reduction in average Secchi depth (Hampton et al 2008) – the depth at which a standard white disk disappears from view. The lack of a visible signal in Secchi depth, even as phytoplankton biomass has increased as evidenced by chlorophyll, highlights the importance of establishing monitoring for "early warning" before a need for monitoring may be perceived visually.

The increases in summertime algal growth are especially interesting in Lake Baikal because, unlike most other lakes, summer is not normally the lake's most productive time of year. Lake Baikal harbors its highest phytoplankton biomass under ice (Moore et al 2009). This phenomenon is dependent on clear snow-free ice that allows enough light to fuel algal growth, to provide substrate for algae that attach to the ice, and to warm near-surface water such that mixing caused by convection is sufficient to suspend the relatively heavy, non-motile diatoms that dominate the algal community at that time of year. The lake's microscopic and macroscopic animals take advantage of this under-ice bounty by consuming both the living algae and also the dead algal filaments that slough to the water column and lake bottom below. Shifts toward greater summer algal productivity would restructure food web interactions that have previously developed around this under-ice algal community.

The composition of the zooplankton community has similarly shifted in concert with warmer lake conditions (Hampton et al 2008). The endemic slow-growing, cold-adapted copepods (Melnik et al 1998) have declined weakly in abundance, and a cosmopolitan group of zooplankton - the cladocerans - has increased significantly. Cladocerans are well known for gaining dominance in warm conditions (Gillooly and Dodson 2000) with relatively high food. They have unusual potential for changing food web dynamics, relative to other zooplankton groups (Sommer and Sommer 2006). Cladocerans are preferred forage for zooplanktivorous freshwater fishes, and have extremely high grazing rates which can depress algal, bacterial and competitor abundance. Additionally, cladocerans can affect the way in which important nutrients cycle within the lake. They sequester more phosphorus than do copepods. Differential sequestration of phosphorus means that copepods typically excrete phosphorus that may be used by algae, while cladocerans do not "fertilize" the algae with phosphorus to the same degree. Results from multivariate autoregressive (MAR) modeling suggest that such a phenomenon might occur in Lake Baikal (Hampton et al 2008). Cladocerans had significant negative relationships with algae, suggesting grazing, while copepods had positive relationships with several algal groups, suggesting that a fertilization effect might have been prominent. Internal cycling of nutrients, such as the feeding and excretion loop described here, can be especially important in large deep lakes where external nutrient "loading" is somewhat less important than it might be in smaller lakes. The trends in zooplankton composition have been relatively subtle numerically and provide additional demonstration of the importance of long-term data collection to achieve the large number of data points necessary to discern pattern from noise.

Changes in ice condition, temperature and precipitation are also likely to affect the top predator in the lake (Moore et al 2009), the Baikal seal, the world's only exclusively freshwater seal. The seals rear their pups on ice where they are protected from predators inside caves that the seals make from snow and ice. Recession of the lake ice would affect the length of season in which the pups can remain in the caves, and changes in precipitation – such as rain rather than snow – and warmer air temperature may cause premature disintegration of the caves as well. To the best of our knowledge, Lake Baikal is the only lake in which both the top predator and also the dominant algae at the base of the food web are both directly dependent on ice, such that Baikal's sensitivity to climate change may be unique (Moore et al 2009).

These long-term trends were embedded in shorter term variability, such as seasonal signals that shifted over time in ways that we initially did not anticipate. The time series that expressed seasonal timing, or phase (Φ) of the annual harmonic of lake temperature variability initially was nothing more than the residuals produced when estimating the long term warming trend in the lake. However, detailed investigation of the phase data revealed large-scale patterns that correlate with multiple indexes of climate variability (Katz et al 2011). On decadal scales, phases were negative, indicating earlier seasons, in 1960 and 1985, and positive (later seasons) in 1970 and 1995. These patterns correlated strongly with variability of zonal winds or jet stream strength. On shorter time scales phases showed correlations with the El Niño Southern Oscillation (ENSO), sea-surface temperature in the Pacific, and these correlations had complex interactions with Pacific Ocean pressure patterns expressed in the Pacific Decadal Oscillation (PDO). Both ENSO and PDO describe conditions associated with jet stream trajectories. Synthesizing these statistical relationships between lake water temperature and hemisphere-scale dynamics of jet stream variability generated a mechanistic model for how variability in diverse global atmospheric dynamics is accumulated and transmitted around the northern hemisphere via the jet stream, ultimately to produce local conditions at lake Baikal (Katz et al 2011).

Aquatic systems worldwide have responded to environmental change (Scheffer et al 2001, Hays et al 2005); the scientific community is racing to catch up with the change that has already occurred, and to predict changes to come. In our Russian-American collaboration we have enjoyed the riches of a very special environmental data set, with a level of temporal and taxonomic resolution that is rare. Retrospective analysis of these data will provide us with many opportunities for the future. First, the data set itself provides a baseline, so that we can put future anthropogenic changes into the context of what has happened over the past half century. Second, analysis of the long-term data can interact synergistically with field and laboratory experiments – for example, inspiring testable hypotheses that can be addressed with field and laboratory approaches to elucidate mechanisms underlying patterns in the long-term data, and also "ground-truthing" experimental results derived from laboratory experiments. Third, the high resolution and quality of the data have allowed us to explore applications of statistical techniques that characterize ecosystem changes on multiple time scales, shifting dynamics of seasonality, and the species interactions through which indirect effects reverberate through ecosystems – issues that are at the heart of many questions environmental scientists and ecologists are addressing as anthropogenic change rapidly reshapes the world around us.

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RÉSUMÉ (ABSTRACT)

Climate change presents complex and uncertain future scenarios in the world's Great Lakes. Major abiotic changes have direct and indirect effects on lake food webs; the nature and extent of such past, present and projected food web changes may be better understood through the analysis of long-term ecological data sets. An excellent opportunity for such analyses exists for subarctic Lake Baikal, the world's most ancient, voluminous, and biologically diverse lake. We have employed several approaches to analyze 60 years of biweekly data collected by 3 generations of a single family of Siberian scientists, to understand climate-associated changes occurring among the plankton that constitute the base of the food web. By applying Time-Frequency analysis, we created two distinct opportunities for analysis: 1) a "de-seasoned" abiotic and biotic data set in which to explore species interactions and responses to larger scale climatic variables, and 2) a time series of transformation properties such as phase of key harmonics, which describe large-scale trends in lake seasonality. With de-seasoned data, we employed multivariate autoregressive (MAR) modeling to explore species interactions in the food web, as well as biotic relationships with temperature and climate indices that can proxy for other climatic variables. Warming was strongly correlated with compositional changes in the plankton, shifts that may affect the manner in which nutrients cycle in the lake. Warming has been accompanied by reduction in ice cover and by increasing depth of the mixed layer of water near the surface, both further altering the physical environment in which Lake Baikal's native cold-adapted biota interact. In addition to the strong long-term warming trend over the past 60 years, we found that seasonality correlates with large-scale climate indices, suggesting that the lake temperature data closely track the dynamics of the jet stream across Siberia.