Lakes as sentinels of climate change

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Abstract

While there is a general sense that lakes can act as sentinels of climate change, their efficacy has not been thoroughly analyzed. We identified the key response variables within a lake that act as indicators of the effects of climate change on both the lake and the catchment. These variables reflect a wide range of physical, chemical, and biological responses to climate. However, the efficacy of the different indicators is affected by regional response to climate change, characteristics of the catchment, and lake mixing regimes. Thus, particular indicators or combinations of indicators are more effective for different lake types and geographic regions. The extraction of climate signals can be further complicated by the influence of other environmental changes, such as eutrophication or acidification, and the equivalent reverse phenomena, in addition to other land use influences. In many cases, however, confounding factors can be addressed through analytical tools such as detrending or filtering. Lakes are effective sentinels for climate change because they are sensitive to climate, respond rapidly to change, and integrate information about changes in the catchment.

Currently, climate change is considered to be one of the most severe threats to ecosystems around the globe (ACIA 2004; Rosenzweig et al. 2007). Monitoring and understanding the effects of climate change pose challenges because of the multitude of responses within an ecosystem and the spatial variation within the landscape. A substantial body of research demonstrates the sensitivity of lakes to climate and shows that physical, chemical, and biological lake properties respond rapidly to climate-related changes (ACIA 2004; Rosenzweig et al. 2007). Fast turnover times from organismal to ecosystem scales in lakes are prerequisite for detecting such rapid changes. Previous studies have suggested that lakes are good sentinels of global climate change because they are sensitive to environmental changes and can integrate changes in the surrounding landscape and atmosphere (Carpenter et al. 2007; Pham et al. 2008; Williamson et al. 2008). However, a more thorough analysis of the potential for lakes to act as sentinels for the rapid rates of current climate change is lacking.

Studies of lakes provided some of the early indications of the effects of current climate change on ecosystem structure and function (Schindler et al. 1996a; Magnuson et al. 2000; Verburg et al. 2003) and the consequences for ecosystem services (O'Reilly et al. 2003). Some climate-related signals are highly visible and easily measurable in lakes. For instance, climate-driven fluctuations in water level have been observed on a broad scale in North America (Williamson et al. 2009), and shifts in the timing of ice formation and thawing reflect climate warming at a global scale (Magnuson et al. 2000). Other signals may be more complex and difficult to detect in lakes, but they may be equally sensitive indicators of climate forcing or equally informative regarding effects on ecosystem services. Available long-term historical records and reconstructions from sediment cores have yielded insight into less visible climate-related changes and provided us with an understanding of the mechanisms that give rise to these changes. Paleolimnological records, in particular, have been crucial in developing climate records over recent geologic timescales, allowing us to interpret current climate change and predict its effects (Smol 2008; Leavitt et al. 2009).

In many ways, lake ecosystems appear to be valid sentinels for current climate change. Lake ecosystems act as sentinels because they provide indicators of climate change either directly or indirectly through the influence of climate

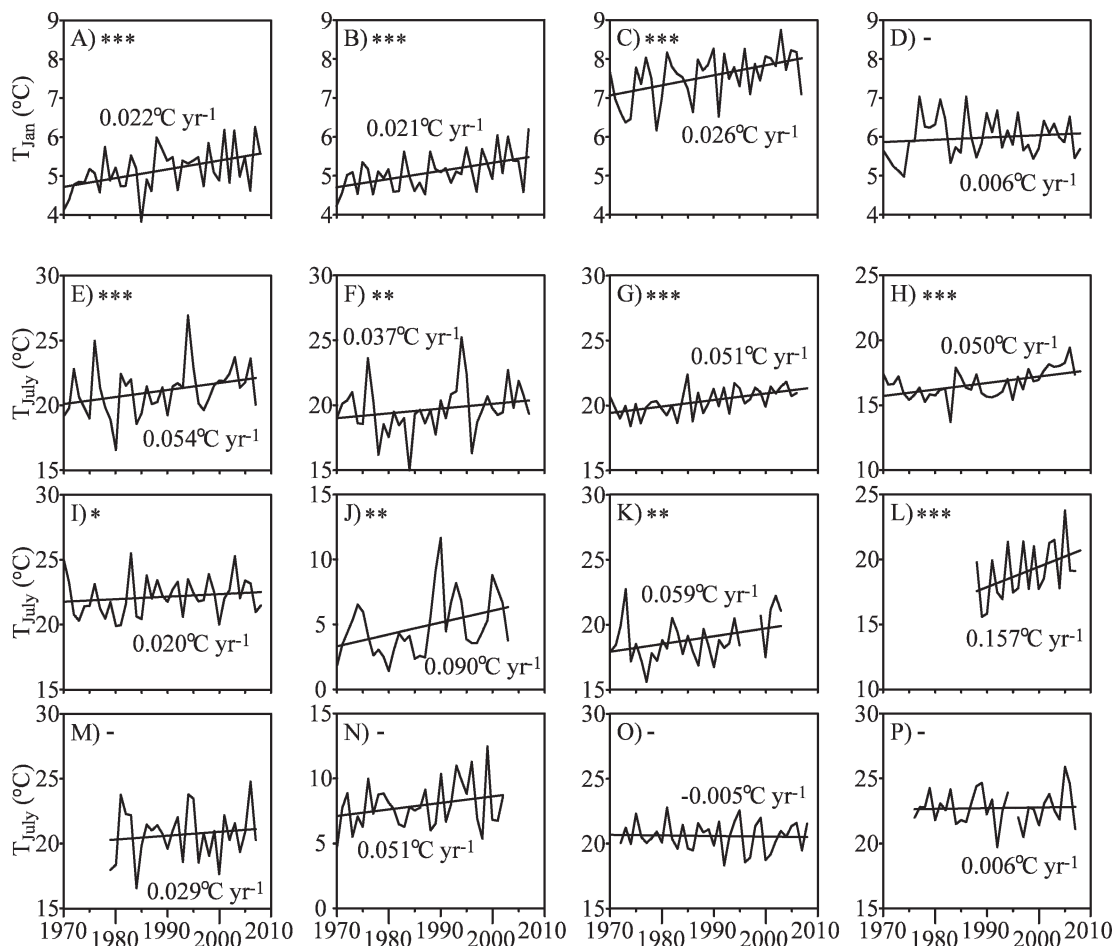* Corresponding author: adrian@igb berlin.de

Fig. 1.   Long term behavior of monthly mean near surface temperatures since 1970 in January (T_{Jan}, A D) and July (T_{July}, E P) in various Northern Hemisphere lakes. (A) and (E) Lake Zürich (Switzerland); (B) and (F) Lake Constance (Germany, Switzerland, Austria); (C) and (G) Lake Washington (Washington); (D) and (H) Lake Tahoe (California, Nevada); (I) Greifensee (Switzerland); (J) Lake Vättern, Edeskvarva basin (Sweden); (K) Lake Mäleren, Görvaln basin (Sweden); (L) Stensjön (Sweden); (M) Müggelsee (Germany); (N) Lake Baikal (Russia); (O) Lake Champlain (Vermont); (P) Blue Chalk Lake (Canada). Monthly means were obtained by spline interpolating measured temperatures at daily intervals and averaging the results. For each lake, the significance level of the Mann Kendall test for the existence of a monotonic trend is indicated by one, two, or three asterisks ($p < 0.1$, $p < 0.05$, and $p < 0.01$, respectively) or a dash (no monotonic trend at the $p < 0.1$ level). The mean rate of change of T_{Jan} or T_{July} is also given, and the long term linear trend is illustrated.

on the catchment. The indicators are measurable response variables, such as water temperature, dissolved organic carbon (DOC), or plankton composition. Specifically, lakes are likely to serve as good sentinels for current climate change because (1) lake ecosystems are well defined and are studied in a sustained fashion; (2) lakes respond directly to climate change and also incorporate the effects of climate-driven changes occurring within the catchment; (3) lakes integrate responses over time, which can filter out random noise; and (4) lakes are distributed worldwide and, as such, can act as sentinels in many different geographic locations and climatic regions, capturing different aspects of climate change (e.g., rising temperature, glacier retreats, permafrost melting). However, the large range in lake morphology, catchment characteristics, and geographic locations implies that we should be cautious about making broad statements about the ability of lakes to capture the effects of the current, rapidly changing climate.

Here, we discuss three critical issues related to the use of lakes as sentinels. The focus of this synthesis paper is to identify limnological variables that respond to climate forcing and to assess the complexity and difficulty associated with using these variables as indicators of climate change. Lake ecosystems are complex, they have many internal feedbacks, and the influence of the catchment can vary depending on geographic location, regional climate, and land use. Do lakes contain accurate indicators that are appropriate for current rates of change? How broadly can these indicators be applied? Can we detect climate-driven changes in the face of other environmental change? First, we identified key properties of lakes and the most appropriate variables that would indicate effects of climate change. To do this, we conducted a review analysis of studies of contemporary climate change and assessed the suitability of a response variable based on its relationship to primary climate drivers, possible confound-

ing effects, and the basic utility (ease of measurement, advantages, and disadvantages) of that indicator. Second, we categorized the appropriateness of specific indicators for different lake types within different climate regions. Finally, we addressed the challenges associated with extracting climate signals from confounding effects. For the purpose of this paper, we excluded reservoirs because their hydrology is largely anthropogenically controlled, and thus their climate-related responses are influenced by specific features of individual systems.

Key response variables and their suitability as indicators of climate change Clearly, there is a diverse set of variables responsive to climate that span a range of physical, chemical and biological properties in lakes (ACIA 2004; Rosenzweig et al. 2007). Some of the most effective indicators of climate change are listed in Table 1. The criteria for choosing those response variables were high synchronicity among lakes, ease of measurement, and their known relevance for ecosystem function. These response variables reflect either a direct influence of climate on the lake or an indirect change via the effect of climate on the catchment. It is beyond the scope of this synthesis paper to address all observed climate-driven changes in lakes around the globe; instead, our purpose is to highlight the advantages and limitations of effective indicators for key lake properties.

Water temperature: Surface and epilimnetic water temperatures, which can be highly correlated with regional-scale air temperatures, exhibit a rapid and direct response to climatic forcing, making epilimnetic temperature a useful indicator of climate change. In many (but no means all) lakes, the epilimnion has undergone recent warming (Fig. 1; Table 1). Epilimnetic temperatures are easy to monitor and reflect warming trends in air temperature in North America (Arhonditsis et al. 2004; Coats et al. 2006), Eurasia (Livingstone 2003; Hampton et al. 2008), and Africa (O'Reilly et al. 2003). In contrast, hypolimnetic temperatures exhibit a much more complex behavior, and they may undergo warming or cooling trends depending on lake morphometry (Gerten and Adrian 2001) and season (Robertson and Ragotzkie 1990; Livingstone and Lotter 1998; Straile et al. 2003). By influencing the density gradient in the water column, vertically heterogeneous changes in water temperature result in long-term changes in the intensity and duration of vertical mixing and stratification, thermal stability, and thermocline depth (Table 1). Long-term changes in thermal structure might in the future be responsible for mixing regimes shifting from polymictic to dimictic, dimictic to monomictic, or monomictic to oligomictic (Boehrer and Schultze 2008; Livingstone 2008). Although long-term changes in thermal structure and mixing regime may require detailed temperature measurements in the water column for their detection, they represent good indicators of climate change because of the directness and sensitivity of their response to climatic forcing. In addition, such long-term physical changes would have severe consequences for nutrient and oxygen concentrations, as well as for the vertical distribution and composition of the biota.

Water level: In nonregulated lakes, water level is a good indicator of climate change because it reflects the dynamic balance between water input (precipitation, runoff) and water loss (evaporation), and the timing of the ice-free season (ACIA 2004; Lenters et al. 2005; Van der Kamp et al. 2008) on timescales ranging from hours to centuries (Argyilan and Forman 2003; Ghanbari and Bravo 2008; Van der Kamp et al. 2008). Measurements of water level are especially useful in the case of closed-basin lakes, where long-term fluctuations in water level can be related to similar fluctuations in large-scale climate oscillations (Rodionov 1994). Possible confounding effects include the influence of groundwater level, along with changes in vegetation and land use in the catchment (Webster et al. 2000; Table 1).

Ice phenology: Although the processes governing the formation and thawing of lake ice depend on multiple interacting meteorological and limnological factors (Gu and Stefan 1990), air temperature is considered to be the dominant variable driving lake-ice phenology (Williams and Stefan 2006). Because individual physical lake properties influence freezing processes much more strongly than thawing processes, the timing of ice-off makes a better direct indicator of climate change than the timing of ice-on (Šporka et al. 2006; Table 1). The use of satellite data to study lake-ice phenology on large spatial scales enhances the utility of the timing of ice-off as a large-scale indicator of climate change (Wynne and Lillesand 1993; Latifovic and Pouliot 2007). However, the relationship between the timing of ice-off and air temperature is not necessarily linear and differs distinctly between colder and warmer geographical regions (Weyhenmeyer et al. 2004). Ice duration can be an appropriate climate-change indicator when ice cover is intermittent, for example, when ice cover forms and thaws several times during a warm winter (Livingstone and Adrian 2009).

Chemical variables: Many of a lake's specific chemical properties represent the terrestrial landscape, and changes in these variables may serve as indicators of terrestrial processes that are otherwise difficult to detect in the more heterogeneous terrestrial ecosystem. Nutrient concentrations and ratios in lakes are likely to be altered as a consequence of changes in terrestrial export related to climatic influences on weathering rates, precipitation, runoff (Sommaruga-Wögrath et al. 1997; Rogora et al. 2003; Bergström and Jansson 2006), fire frequency (Kelly et al. 2006; Westerling et al. 2006), or terrestrial primary productivity (Boisvenue and Running 2006). Nutrient concentrations can also be affected by internal processes related to changes in thermal structure and/or primary productivity (Jeppesen et al. 2005; Wilhelm and Adrian 2008). The pH, ionic strength, ionic composition, and conductivity are very sensitive and easily measurable indicators of changes in weathering rate, as well as water balance. For many lakes, there can be challenges in disentangling the roles of internal and catchment changes with respect to water chemistry, which may be further complicated by confounding factors such as eutrophica-

Table 1. Summary of key response variables to climate change for physical, chemical, and biological lake characteristics, and major underlying processes, mechanisms, and climate drivers along with comments on confounding factors, advantages, and disadvantages. Abbreviations are as follows: PP, precipitation; AT, air temperature; WT, water temperature; WS, wind speed; CC, cloud cover; RH, relative humidity; TKE, turbulent kinetic energy; DOC, dissolved organic carbon; A, advantages; D, disadvantages.

Lake properties	Response variables	Processes or mechanisms	Climate-related drivers	Confounding factors and comments	Advantage or disadvantage/ utility or limitation	References
Hydrology	Water level	Runoff, dilution, and transport of elements, evapotranspiration	PP, AT, WS, CC, RH	Catchment characteristics and disturbances; already used as climate indicator by international assessments (Rosensweig et al. 2007)	A: easily measured D: many lakes are regulated	Rodionov (1994); ACIA (2004); Jöhnk et al. (2004)
Temperature	Epilimnetic temperature	Radiative and nonradiative heat exchange across the air–water interface	AT, WS, CC, RH	Turbidity, water color; already used as climate indicator by international assessments (Rosensweig et al. 2007)	A: easily measured D: large short-term variations; does not always correlate highly with air temperatures in small lakes	Livingstone and Dokulil (2001); O'Reilly et al. (2003); Keller (2007); Hampton et al. (2008)
	Duration of summer stratification	Shifts in the timing of spring and fall mixing events	AT, WS, CC, RH	Can be related to ice phenology	A: integrates climate signal over longer timescale (several months) D: requires high-resolution data both spatially and temporally	McCormick and Fahnenstiel (1999); Livingstone (2003)
	Depth of the thermocline	As thermal stability: a product of the opposing effects of PE and TKE	AT, WS, CC, RH	In small lakes dependent on transparency	A: good estimate for certain habitat refuges D: dependent on lake morphometry; precise definition requires temperature profiles with high spatial resolution	Schindler et al. (1996a); Coats et al. (2006); Tanentzap et al. (2008)
Ice phenology	Ice-out	Thawing in spring	AT, PP, WS, CC, RH	Thawing of ice and snow are complex; PP as rain enhances thawing; PP as snow retards thawing	A: directly influenced by meteorological forcing; spatially very coherent among different lakes over large areas; tightly related to air temperature D: definition of ice-off depends on the observer; ill-defined if the ice thaws and refreezes during winter	Magnuson et al. (2000); Latifovic and Pouliot (2007)

Table 1. Continued.

Lake properties	Response variables	Processes or mechanisms	Climate-related drivers	Confounding factors and comments	Advantage or disadvantage/utility or limitation	References
	Ice duration	Single or multiple occurrences of ice-on and ice-off	AT, WS, CC, RH	Ice-on is critically dependent on individual lake morphometry and lake physics	A: integrates climate signal over longer timescale; detectable by remote sensing on large spatial scale D: if intermittent, must be observed each day	Magnuson et al. (2000); Latifovic and Pouliot (2007)
Transparency	DOC	Runoff, permafrost melting, changes in terrestrial C dynamics, shifts in vegetation patterns, glacier retreat	AT, PP, CC, RH, WS, atmospheric deposition	Modified by in-lake, catchment processes and recovery from acidification	A: integrates multiple responses in lake processes and catchment processes D: site-specific; i.e., different lakes may display opposite patterns in response to climate change	Yan et al. (1996); Williamson et al. (1999); Pienitz and Vincent (2000); Freeman et al. (2004); Frey and Smith (2005); Keller et al. (2005)
	Turbidity	Scattering by living and nonliving particulates; glacial melting, changes in hydrology	PP, AT, CC, glacier retreat	Modified by runoff, physical disturbances, and trophic status	A: easily measured D: site-specific	Smith (1978); Leavitt et al. (2003)
	Secchi depth phenology	Absorption by dissolved substances and particulates, scattering by particulates	AT, WS, CC	Biological interactions i.e, grazing	A: proved efficacy as indicator; easily measured; integrates a number of processes within the food web D: affected by trophic state	Gerten and Adrian (2000); Straile (2002); Huber et al. (2008)
Chemistry	Oxygen	Ice, mixing, metabolism	AT, WS	Confounded particularly by changes in trophic status	A: hypolimnetic oxygen concentrations provide strong indicator for internal nutrient dynamics and habitat refuges D: site-specific; particularly trophic status	Hanson et al. (2006); Jankowski et al. (2006); Wilhelm and Adrian (2008); Winder and Hunter (2008)

Table 1. Continued.

Lake properties	Response variables	Processes or mechanisms	Climate-related drivers	Confounding factors and comments	Advantage or disadvantage/ utility or limitation	References
	Conductivity or salinity, pH or alkalinity	Dilution, evaporative concentration	AT, PP, atmospheric deposition WS, CC, RH,	Droughts can lead to subsequent reacidification; lakes dominated by surface-water or groundwater inputs may respond differently to changes in water supply	A: easily measured D: site-specific	Yan et al. (1996); Webster et al. (1996)
Autecology	Phenology	WT, timing of ice-out, stratification onset	AT	Trophic state; already used as climate indicator by international assessments (Rosensweig et al. 2007)	A: applies to organisms with a distinct seasonality D: needs long-term data at high temporal resolution; site-specific	Adrian et al. (1999); Weyhenmeyer et al. (1999); Winder and Schindler (2004a,b)
	Life history	Degree days, winter severity	AT	Food availability, predation	A: includes juvenile and adult stages D: not easily detectable; limited long-term records	Adrian et al. (2006); Seebens et al. (2007)
Community structure	Algal blooms	WT, stratification	AT, WS	Trophic state	A: applicable for specific algal taxa D: applies mostly to productive lakes	Huisman et al. (2004); Jöhnk et al. (2008)
	Changes in relative species composition	WT, UV exposure, stratification intensity, transparency	AT, WS	Trophic state, species interactions	A: identifies winners of climate change D: ways in which species interactions will likely change with warming are incompletely understood; species-specific thermal tolerances in nature are often not known and may be modified by other factors	Strecker et al. (2004); Adrian et al. (2006); Marinone et al. (2006); Rühland et al. (2008); Winder and Hunter (2008)
	Primary productivity	Stratification length and intensity, degree days, ice-free period	AT, WS, CC	Trophic state, transparency, already used as indicator of climate change (Rosenzweig et al. 2007)	A: particularly relevant for arctic, alpine, and subalpine lakes; detectable by remote sensing on large spatial scale D: site-specific; difficult to measure	O'Reilly et al. (2003); Michelutti et al. (2005)

Table 1. Continued.

Lake properties	Response variables	Processes or mechanisms	Climate-related drivers	Confounding factors and comments	Advantage or disadvantage/ utility or limitation	References
	Invaders	Temperature, degree days, transparency	AT, PP	Human activity, habitat modification, chemical environment	A: documents change over large spatial scale D: only applicable for lakes with data of high taxonomic resolution	Holzapfel and Vinebrooke (2005)
Habitat structure	Habitat refuge	WT, vertical temperature and oxygen gradients; UV	AT, WS	Lake morphometry, transparency	A: if habitat diminishes, it is a far-reaching indicator D: species-specific	De Stasio et al. (1996); Tartarotti et al. (2001); Jansen and Hesslein (2004)

tion, acidification, or atmospheric nitrogen deposition (Hessen et al. 2009). This is more likely to be the case for biologically reactive elements than for conservative elements (Na, Mg, and even Ca in lakes that do not experience weathering events).

Dissolved organic carbon (DOC) concentrations can also serve as an indicator, and they may be particularly appropriate for detecting changes within the terrestrial environment (Tranvik et al. 2009). DOC integrates multiple responses within the lake, such as water transparency (particularly in the ultraviolet range), heat absorption, and lake metabolism (Williamson et al. 1999), as well as changes observed in the catchment related to increased run-off, permafrost melting, shifts in vegetation, and changes in wetlands (Evans et al. 2006; Benoy et al. 2007; Keller et al. 2008), and increased CO_2 concentrations (Freeman et al. 2004; Tables 1, 2). Allochthonous DOC concentrations can be a key indicator of catchment processes, particularly in boreal catchments, where DOC is generally dominated by allochthonous material, and increasing inputs associated with climate change are having strong effects on lake ecosystems (Parker et al. 2008). The disadvantages of DOC as an indicator of climate change are that it can also be influenced by atmospheric deposition (Monteith et al. 2007; Mladenov et al. 2008; Weyhenmeyer 2008a) and eutrophication (Nürnberg and Shaw 1998) and that long-term measurements are scarce.

Oxygen concentrations in lakes can indicate climate shifts because oxygen levels are strongly influenced by temperature and thermal structure (Hanson et al. 2006; Table 1). For example, the extremely warm European summer of 2003 resulted in a long period of thermal stratification and increased hypolimnetic oxygen depletion in some Swiss lakes (Jankowski et al. 2006). When applicable, hypolimnetic oxygen concentrations have added value as indicators of climate change because they have widespread consequences for internal nutrient loading (Pettersson et al. 2003), habitat size, and refuge availability (De Stasio et al. 1996; Jansen and Hesslein 2004).

Biota: Interactions between climate change and lake biota are complex because other factors such as resource availability, density dependence, and predation strongly control the abundance, distribution, and size of the biota. In addition, responses are often species-specific and vary among ecosystems (Baines et al. 2000; Adrian et al. 2006). Despite these difficulties in using organisms as indicators for climate change, some widespread climate-related responses of lake biota have emerged, and the mechanisms involved in climate-related changes are becoming better understood. Planktonic organisms have been used widely as indicators of ecosystem change, and because these relatively short-lived organisms respond rapidly to subtle thermal changes, they are also useful indicators of climate change. Phytoplankton and zooplankton communities in many lakes have been relatively well-documented over extended time periods, and these records are useful for extracting climate-related responses.

Changes in spring and early summer phenology can provide a good reflection of climatic shifts (Straile 2002;

Table 2. Summary of indicators of climate change for lakes of various types. Lakes are defined by characteristics of their (A) climate and basin morphometry, and (B) location catchment characteristics. Arctic lakes are defined as those existing in regions with permafrost, or at higher latitudes; boreal lakes are high latitude lakes with catchments composed mostly of coniferous forest; alpine lakes are those located above the tree line; temperate lakes and tropical lakes are only defined by their climate zones; arid lakes include those in Mediterranean and desert climates, or those located in grassland regions. Hypothesized or observed directions of changes in climate related variables, indicators, and ecosystem services related to the response variables are indicated by + (positive) or (negative). Indicators responding directly to the climate drivers are in line with those drivers. Indicators that are indirectly related to the climate driver are listed below the directly affected indicator. Ecosystem services are in line with the relevant indicators. Abbreviations: OM, organic matter; DOM, dissolved organic matter; strat, stratification; temp, temperature; TP, TN, total phosphorus and nitrogen, respectively; $p\mathrm{CO_2}$, partial pressure of carbon dioxide; Chl, chlorophyll *a*; UV B, ultraviolet B radiation (280 315 nm).

Climate region	Catchment or mixing state	External driving variables	Indicators	Affected ecosystem services
Direct effects of climate across lake surface				
Arctic+alpine+ boreal+temperate		+/ Snow fall +Air temp	+/ Snow pack +Ice free period	Albedo, water storage +Productivity
Arctic	Monomictic, polymictic	+Air temp	+Summer stability Bottom O_2	Habitat, +greenhouse gases (+CH_4)
Arctic+boreal+ temperate+arid	Polymictic	+Air temp	+Surface temp +Strat frequency period	Habitat, +climate indicator Productivity, +nutrient retention
Boreal+temperate	Dimictic	+Winter air temp	Winter ice period +Winter bottom O_2 Spring PO_4	Recreation, +/ habitat +Habitat Productivity
Boreal+temperate+ arid	Dimictic, monomictic	+Air temp	Timing of stratification +Stability +Cyanobacteria	Fish production Water quality, recreation
Temperate+arid+ tropical	Dimictic, monomictic, oligomictic	+Air temp	+Strat period, +stability Surface TN, TP Bottom O_2, +H_2S +Deep NH_4, PO_4	Productivity, +recreation Habitat Nutrient storage
Arid+tropical	Meromictic	+Evaporation, inflow	+Surface conductivity Stability +Deep water O_2 +Surface H_2S, CO_2 emissions	 +Habitat Human health
Tropical		+Air temp	+Surface temp	Habitat
Indirect effects of climate via catchment				
Arctic	Tundra	Permafrost +OM leaching from soil +Weathering of till	Water level +$p\mathrm{CO_2}$ +Chl Benthic PPR	Habitat, regional heat capacity +Greenhouse gases +Productivity Habitat
Alpine	Rock, meadow	+Air temp +Shifting tree line Glaciers	+Ice free period +Annual UV B DOM +DOM UV B	+Productivity Habitat, productivity C storage +Productivity +Habitat
Arid	Chaparral, desert, grassland	Regional water balance Nutrient inputs	Water level +Conductivity, alkalinity Chl, +water clarity	Water storage Water quality Productivity, +water quality
Boreal+temperate	Forested	+Soil decomposition, fire +/ Precipitation (soil flushing)	+DOM +/ DOM	Recreation, productivity, +carbon storage +/ Recreation, +/ productivity, +/ carbon storage
Temperate	Urban, agricultural	+/ Precipitation +Air temp	+/ Nutrients +Stability +Cyanobacteria Bottom O_2	/+Water quality Water quality, recreation Habitat, +greenhouse gases (N$_2$O)

Blenckner et al. 2007; Rusak et al. 2008; Table 1). For zooplankton, phenological shifts are usually restricted to fast-growing plankton (but *see* Winder and Schindler 2004*a*, Seebens et al. 2007), whereas longer-lived plankton may respond in more complex ways (Winder and Schindler 2004*b*; Adrian et al. 2006). For longer-lived organisms with a complex life cycle, climate warming can accelerate ontogenetic development, which can cause a shift in life history, as has been shown for fish and copepod species (Schindler et al. 2005; Adrian et al. 2006; Winder et al. 2009). Spring migrations for several anadromous fish species are happening earlier, and this timing can also be used as an indicator of climatic changes (Quinn and Adams 1996).

Growth rates, abundance, and species composition can each be considered an indicator of climate change. Given sufficient resource availability, increasing temperatures generally accelerate growth and development rates of individual organisms, although changes in absolute abundances tend to be species-specific (Adrian et al. 2006; Reist et al. 2006; Blenckner et al. 2007). Changes in species composition have been used as a climate indicator on longer geological timescales (Rühland et al. 2008), as well as in contemporary studies. For example, at higher temperatures, bloom-forming cyanobacteria have a competitive advantage over other phytoplankton groups (Jöhnk et al. 2008; Wagner and Adrian 2009*b*). Similarly, stronger vertical stratification can cause shifts in phytoplankton species composition (Verburg et al. 2003; Strecker et al. 2004; Winder and Hunter 2008). Shifts in phytoplankton species composition, especially among those taxonomic groups that are sensitive to temperature and mixing, such as cyanobacteria, diatoms, and flagellates, can be considered indicators of climate-induced enhancements in thermally stratified conditions (Table 1). Changes in fish-species distributions, abundance, and community structure are also indicative of climate effects, particularly as available habitat for cold-water species contracts (Gunn 2002; Reist et al. 2006).

Other climate-related responses of lake biota may be effective indicators for particular systems. These include responses such as changes in primary productivity (O'Reilly et al. 2003; Michelutti et al. 2005), zooplankton body size (Moore et al. 1996), increased bacterial cell densities (Rae and Vincent 1998), and benthic net photosynthesis and dark respiration rates (Baulch et al. 2005). Finally, climate may also affect species diversity and composition through the invasion of non-native species that expand their geographical range as water temperatures warm (Rahel and Olden 2008). Detailed knowledge of invasive species' life-history requirements would be important for evaluating their efficacy as a climate indicator (Table 1). However, all of these responses are often lake-specific and can be difficult to predict on larger scales.

Geographic variation in the use of lakes as sentinels
Climate-driven changes will have different effects on lakes depending on geographic location, elevation, morphometry, climate, vegetation, and land use. For example, in forested lakes in temperate and boreal zones, DOC concentrations may best reflect climate-mediated changes in soil processes such as soil decomposition rates and the flushing of soil organic matter. In agricultural catchments, however, changes in precipitation and decomposition may primarily alter the import of nutrients into water bodies. In Arctic ponds, cation concentrations (and strontium isotopes) are sensitive indicators of melting permafrost, which exposes previously unweathered glacial till in the catchment to weathering (Hobbie et al. 1999; Prowse et al. 2006). The water levels of Arctic lakes have also proven to be a sensitive indicator of the northern extent of permafrost (Smith et al. 2005; Marsh et al. 2009). In contrast, lakes in arid and tropical environments experience shifts in water level and conductivity related to swings in water balance and evapo-concentration (Awange et al. 2008; Croley and Lewis 2008; Van der Kamp et al. 2008).

The utility of a specific indicator depends on the characteristics of the lake in which it is measured (Table 2). At the simplest level, characteristics of the lake and the catchment influence both the sensitivity of the indicator variable to climate change and the amount of background variability to which the indicator is subject. For example, in very small lakes with low heat capacity, surface-water temperature responds quickly to radiative and evaporative heat exchange and solar irradiance (Gerten and Adrian 2001). While high sensitivity is a useful characteristic for an indicator, it also leads to more of the same high-frequency "noise" that masks long-term trends in climate data. One may postulate, therefore, that there is a lake size for which the combination of noise reduction and sensitivity is optimal. A similar line of argument could be constructed for an optimal hydrologic residence time when using water chemistry to detect climate-mediated changes that result from alterations in catchment inputs. Certainly there appears to be an optimal combination of landscape position and residence time when choosing lakes to use for assessing the effect of climate on groundwater flows in response to drought (Webster et al. 1996; Baines et al. 2000).

A lake's internal physical structure, morphometry, hydrological setting, and biota can alter the primary mechanisms by which climate affects a given indicator variable. As a result, a variable that shows one response to climate change in one lake may exhibit a very different response in another (Weyhenmeyer 2008*b*). For example, in short-residence-time boreal lakes, DOC may most closely reflect variations in inputs related to the production of DOC in catchment soils and its subsequent export to streams or groundwater. Melting permafrost, longer growing seasons, increased soil temperatures, and greater precipitation in boreal regions might lead to increases in DOC for such lakes. In lakes with longer residence times, loss processes such as bacterial degradation (Tranvik 1992), photo-oxidation (Lindell et al. 1995; Bertilsson and Tranvik 2000), aggregation, and sedimentation (Von Wachenfeldt et al. 2008) become more important. To the extent that water temperature and the duration of the ice-free period affect these loss processes (Sommaruga et al. 1999; Reche et al. 2000), the expected increase in DOC with climate change may be dampened or even reversed in these longer-residence-time lakes. Trends in mineral nutrient levels may also be expected to differ among lakes based on the processes driving them. In stratified lakes, warming is

likely to decrease productivity by increasing the intensity, extent, or frequency of stratification and thereby reducing internal loading (O'Reilly et al. 2003; Coats et al. 2006). In other lakes, the effects of climate change may result in the delivery of new nutrients from the catchment or enhanced internal recycling (McKee et al. 2003; Wilhelm and Adrian 2008; Wagner and Adrian 2009*b*).

Differences among lakes, as outlined in Table 2, provide both complications and opportunities with respect to the use of lakes as sentinels of climate change. At one level, the effective use of indicator variables will depend critically on identifying the lake variable combinations that are most sensitive and least affected by other confounding processes. This identification depends to some extent on a sound quantitative knowledge of the mechanistic linkages between climate variables and lake response variables and suggests that multiple indicator variables may be necessary (Table 2). Linking changes in climate to changes in variables such as DOC, nutrient concentrations, and algal productivity may be demonstrable, but the relationship is not always well understood for some lakes. In these situations, the existence of variability among lakes represents a significant opportunity to understand the linkages between climate and these indicator variables, as well as the ways in which these linkages are altered by catchment and basin characteristics. Comparisons of a single indicator variable across a spectrum of different lake types affected by a common climate signal can clarify the sensitivity of an indicator variable to climate and highlight contextual variables that influence that sensitivity (Baines et al. 2000; Webster et al. 2000; Pace and Cole 2002).

Attributing changes to climate effects Lakes are commonly affected by multiple interacting stressors (Christensen et al. 2006; Yan et al. 2008), which could confound the signals from climate change. Even lake surface temperature, which is usually tightly linked to air temperatures, may not always reflect the direct effects of climate warming (Fig. 1). For example, reduced wind speed as a consequence of tree planting combined with an increase in DOC concentration due to deacidification resulted in a decrease in the whole-lake temperature of Clearwater Lake, Ontario, despite a regional increase in air temperatures (Tanentzap et al. 2008). In many relatively small lakes, air temperatures alone often explain only a relatively small portion of the observed variation in lake surface temperatures (Fee et al. 1996; Keller 2007). The problem of confounding factors increases when considering chemical or biological response variables. Lakes in various regions around the globe have been subject to changes in land-use patterns (Pham et al. 2008), nutrient inputs (eutrophication and oligotrophication; Jeppesen et al. 2005; Van Donk et al. 2008), and the deposition of sulfur and nitrogen oxides (acidification and deacidification; Schindler et al. 1996*b*). These processes may interact in a nonlinear fashion with climate change or may neutralize climate effects (Wagner and Adrian 2009*a*).

Eutrophication: The effects of eutrophication and oligotrophication on lakes will diminish their utility as sentinels of climate change. Both the direct and indirect effects of warmer water temperatures and increased nutrient availability due to eutrophication may enhance process rates and complicate the use of oxygen concentrations (Matzinger et al. 2007), phytoplankton phenology (Thackeray et al. 2008), phytoplankton community composition (Paerl and Huisman 2008), zooplankton community composition (Straile 2005), and overall community composition as indicators of climate change. Additive effects of eutrophication with climate can be highly complex when food-web interactions are involved (Seebens et al. 2007; Van Donk et al. 2008), and the processes involved in responses to climate change and eutrophication are intertwined. For example, changes in phytoplankton density due to eutrophication and oligotrophication will alter water transparency, thereby modifying the thermal structure of lakes (Jones et al. 2005). Furthermore, the effects of climate change may be partially based on processes similar to those associated with eutrophication because warming might increase phosphorus concentrations through increased internal loading (Jensen and Andersen 1992), especially in concert with extended anoxic conditions (Wilhelm and Adrian 2008).

Acidification: Climate change also interacts with acidification and recovery from acidification (Sommaruga-Wögrath et al. 1997). Acidification reduces DOC concentrations in lakes (Schindler et al. 1996*b*; Yan et al. 1996), thereby altering transparency of the water column. Hence, acidification (or deacidification) will affect thermal structure, especially in small lakes (Fee et al. 1996), through changes in the depth of the mixed layer (Yan 1983; Mazumder and Taylor 1994) and changes in thermal gradients, which affect the stability of the water column (Gunn et al. 2001; Persson and Jones 2008). In addition, changes in DOC concentration due to changes in acidification status will have an important effect on ultraviolet (UV) penetration (Schindler et al. 1996*b*; Yan et al. 1996). Hence, acidification and deacidification may interfere with the use of physical, chemical, as well as biological variables as indicators of climatic change. In particular, in regions affected by historically high acid deposition, the recovery of lakes from acidification will need to be considered in assessments of climate-change effects (Keller et al. 2005; Monteith et al. 2007).

Dealing with confounding factors Confounding factors such as eutrophication, acidification, nitrification, and the equivalent reverse phenomena generally fluctuate less rapidly than climatic variables. This difference in behavior can be utilized to distinguish between climatic forcing and confounding factors by removing trends and low-frequency fluctuations from relevant time series by detrending or high-pass filtering, and analyzing only the remaining, higher-frequency fluctuations that are driven mainly by external physical forcing. A detrending approach has been used successfully in studying the influence of climate on the population dynamics of a calanoid copepod (Seebens et al. 2007) and on the influx of nutrients in lakes of the English Lake District (George et al. 2004). Likewise, the effect of climate on nitrate concentrations in lakes was revealed after accounting for the effects of a long-term decrease of

atmospheric nitrate deposition in a multiple regression model (Weyhenmeyer et al. 2007). Jankowski et al. (2005) used high-pass filtering to remove long-term nonlinear anthropogenic effects from nitrate time series in order to focus on the effects of comparatively high-frequency climatic forcing. Detrending is also a useful option when separating the effects of nonclimate stressors from climate effects due to climate oscillations such as El Niño Southern Oscillation, the North Atlantic Oscillation, or the Pacific Decadal Oscillation, thus allowing these large-scale climatic phenomena to be used as proxies for the effects of climate change (George et al. 2004; Jankowski et al. 2005; Blenckner et al. 2007). Detrending or high-pass filtering will also remove any long-term trend in the data that might result from climate warming, which suggests that in lakes with ongoing changes in other stressors, many chemical and biological state variables will be of only limited use as indicators of climate change. When this is the case, mechanistic simulation models may help to disentangle the effects of warming from other stressors (Elliott and May 2008; Huber et al. 2008). Hydrodynamic models can also be used to distinguish between the effects of changes in air temperature and changes in wind speed and light attenuation on the thermal regimes of lakes (Tanentzap et al. 2008). Simulation models can quantify the effect sizes of confounding variables on response variables. For example, Schalau et al. (2008) showed that a 10-fold increase in algal carrying capacity mimicking eutrophication had only a minor effect on the timing of maximum *Daphnia* abundances and the clear-water phase as compared to changes in the onset of vernal warming.

Overall, our synthesis indicates that lakes have a strong potential as sentinels of current climate change and, as such, can contribute to our understanding of global climate effects. We identified a suite of response variables that can act as effective indicators of climate change. These indicators have response times that allow them to reflect the rapid rates of current changes in climate and to reflect changes in many different properties of lake ecosystems (Table 1). Not all indicators can be used broadly across all lakes; there are certain indicators that are particularly suitable for different lake types and regions (Table 2). Even so, the global distribution of lakes contributes substantially to their utility as sentinels and allows them to stand out from many other current indicators of climate change that are typically biome-specific, such as the retreat of alpine glaciers, the melting of permafrost, or the reduction in sea ice. As sentinels, lakes provide a way to detect and monitor the effects of climate change at the ecosystem scale in locations that are under-represented in climate studies or are influenced by other environmental changes.

Part of the strength of using lakes as sentinels comes from the fact that lakes are able to provide information about the effects of climate change on the terrestrial landscape as well as the lake itself. By using combinations of indicators and by comparing responses among lakes, it is possible to tease apart the effects of climate on the catchment from those on the lake. The value of lakes for detecting changes within the terrestrial landscape enhances their use as sentinels, particularly for cases when it would otherwise be difficult to determine these changes in the catchment, i.e., weathering rates. By using lakes as sentinels of catchment changes, we may be able to increase our mechanistic understanding of terrestrial aquatic linkages.

The efficacy of lakes as sentinels of climate change depends upon our understanding of internal lake processes. For the key indicators, listed in Table 1, we have a reasonably solid understanding of the mechanistic link between climate and lake response that allows us to use these indicator variables effectively. The application of these indicators to different lakes depends on our ability to distinguish the signal from noise, which can be affected by interannual lake variability, terrestrial aquatic linkages, species life histories, and other factors. Therefore, the use of lakes as sentinels not only allows us to detect global effects of climate change, but it can also further our understanding of ecosystem processes in lakes.

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