Lakes and streams as sentinels of environmental change in terrestrial and atmospheric processes

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Recent advances in our understanding of the importance of continental- to global-scale connectivity among terrestrial and aquatic ecosystems make consideration of aquatic–terrestrial linkages an urgent ecological and environmental issue. Here, we describe the role of inland waters as sentinels and integrators of the impact of humans on terrestrial and aquatic ecosystems. The metabolic responses of lakes and streams (ie the rates at which these systems process carbon) are proposed as a common metric to integrate the impacts of environmental change across a broad range of landscapes. Lakes and streams transport and alter nutrients, contaminants, and energy, and store signals of environmental change from local to continental scales over periods ranging from weeks to millennia. A carefully conceived and well-integrated network that includes monitoring and experimental approaches to terrestrial–aquatic connectivity is critical to an understanding of basic ecosystem-level processes and to forecasting and mitigating future environmental impacts at the continental scale.

Front Ecol Environ 2008; 6(5): 247–254, doi:10.1890/070140

Aquatic ecosystems are particularly vulnerable to environmental change and many are, at present, severely degraded. Ironically, this vulnerability makes aquatic ecosystems good sentinels and integrators of environmental change at scales ranging from local (eg extinctions of endemic species) to global (eg climate change).

In a nutshell:

- Inland waters supply essential ecosystem services to human populations by providing water for drinking, bathing, industry, and recreation; they are also a hotspot of biodiversity, but their integrity is threatened
- Inland waters are sentinels and integrators of terrestrial and atmospheric processes, because they are integrally linked with changes in the terrestrial landscape and are highly connected through the transport and storage of water, nutrients, contaminants, and energy
- The metabolism of inland waters provides a fundamental metric of cross-ecosystem connectivity that responds to natural and human disturbances across scales, from changes in riparian zones to global-scale climate change
- A continental-scale network, involving both observational and experimental research in inland waters, is necessary to understand human impacts on terrestrial and aquatic ecosystems and the critical services that they provide

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Freshwater fish, mussels, and crayfish are among the most highly endangered groups of animals on the planet (Ricciardi and Rasmussen 1999), and rates of decline in biodiversity are higher for freshwater than for either terrestrial or marine organisms (Jenkins 2003). Even some of the most pristine alpine lakes and streams, which provide drinking water supplies for much of the world, are threatened (Figure 1). As a result, Americans spend billions of dollars annually to avoid consumption of tap water – over 5 billion gallons of bottled water were purchased in 2000 (US EPA 2003). "No swimming" signs warn of unsafe waters and harmful algal blooms along beaches that border lakes, rivers, reservoirs, and coastal oceans. Consumption warnings have been issued for fish in 44 states in the US, due to levels of mercury contamination that can cause neurological and developmental problems in children (Driscoll *et al.* 2007). Oxygen depletion in both lakes and coastal environments has caused extended anoxic "dead zones", where fish kills and mortality of other benthic organisms are common (Dybas 2005). Water-borne pathogens, including the bacterium that causes cholera (*Vibrio cholerae*), have been found in recreational waters such as the Chesapeake Bay (Huq *et al.* 1983), and severe and potentially fatal intestinal parasites such as *Cryptosporidium parvum* are estimated to be present in up to 55% of surface waters and 17% of drinking water supplies in the US (Rose *et al.* 1991). This vast array of largely human-induced problems in lakes and streams necessitates a continental-scale network to effectively address such environmental challenges.

Concurrently, global climate change is transforming aquatic ecosystems (Poff *et al.* 2002). The period of winter ice cover on lakes and rivers is a week or two shorter

Figure 1. *Arikaree Glacier and its meltwater alpine lake in the headwaters of a protected watershed in the Rocky Mountains of Colorado. This watershed serves as a municipal water supply for the Boulder metropolitan area. Such alpine lakes have very short ice-free growing seasons, low nutrients, and very little vegetation in the surrounding terrestrial watershed, making them very vulnerable to contaminants entering from the surrounding airshed. Such high elevation environments are also experiencing some of the most rapid responses to climate change.*

than it has been in the past (Magnuson *et al.* 2000) and, within a few decades, the Arctic Ocean is likely to be completely ice-free, with potentially severe feedbacks for global climate regimes (Johannessen *et al.* 1999). All of these are signs that the aquatic ecosystems on which we depend are undergoing serious changes at local, regional, and continental scales.

The most important questions are: how do we begin to understand the causes of such large-scale changes in aquatic ecosystems, and how can we forecast and prepare for those changes? These shifts in our aquatic ecosystems are driven largely by human impacts on terrestrial and atmospheric systems. While human hydraulic modifications, channelization, water abstraction, and impoundments also contribute greatly to the alteration of inland waters, here, we address ecological issues related to three primary large-scale environmental forcings: changes in climate, land use, and nitrogen deposition (Peters *et al.* [2008] in this issue). We use these three major forcings as a framework to outline the role that inland waters play as sentinels and integrators of environmental change in terrestrial and atmospheric processes. For clarity, we refer collectively to flowing waters (eg streams, rivers, wetlands) as "streams", and to standing waters (eg ponds, lakes, reservoirs) as "lakes". Thus, we use "lakes and streams" to include all continental inland waters except groundwater. While there are a number of water-quality networks that monitor inland waters in the US, these networks focus on pollutants and primary nutrients. Long-term estimates of metabolism in streams indicate seasonal, daily, and annual changes in rates (Roberts *et al.* 2007). Thus, occasional measures of concentrations do not provide enough information to protect the integrity of the process-based ecosystem services provided by lakes and streams on continental scales (Dodds 2006b).

The role of lakes and streams as sentinels and integrators

Just as the circulatory and respiratory systems give medical doctors critical information on personal health, the metabolic and other ecosystem characteristics of streams and lakes that supply and receive water from the surrounding landscape provide critical information on the health of terrestrial and atmospheric processes. The most integrative signals of environmental change are likely to be found at the lowest points in the landscape (WebFigure 1). Whether it is the cycling or fate of nutrients, organic carbon, contaminants, or pathogens, the water that drains these systems provides critical signals of past and present disturbance that, in turn, provide the foundation for forecasting future impacts. In addition to being the most critical resource for human civilization, water is also one of the primary conduits transporting contaminants and pathogens across the landscape. Water is the lifeblood of the biosphere, and lakes and streams are central to any continental-scale approach designed to understand environmental change.

We argue that metabolism should be a primary response variable if we are to understand the impacts of climate change, land use, and nitrogen deposition (Table 1). Metabolism refers to the rates at which whole ecosystems, or their component parts, process carbon through primary production and respiration (WebFigure 2). Metabolism is perhaps the most fundamental of ecosystem processes and is influenced directly by changes in climate, land use, and atmospheric deposition. Lakes and streams consume carbon dioxide and produce oxygen through photosynthesis, and reverse this process through respiration and fermentation of organic carbon. The majority of the respired carbon in many streams and lakes derives from the surrounding terrestrial ecosystems (Cole *et al.* 2006). Climate change, land use, and nitrogen deposition can alter ecosystem metabolism in fundamental ways: lakes and streams are integrators, sentinels, and, to some extent, regulators of environmental change. For example, whole-lake metabolism is directly influenced by the relative balance of external loadings of nutrients and dissolved organic carbon (Hanson *et al.* 2003). Changes in these loadings due to alterations in climate, land use, or atmospheric deposition will influence the metabolic balance of lakes. Understanding the resistance, resilience, and directional responses of lakes and streams to environmental change is also crucial to effective management.

Aquatic ecosystems integrate local watersheds that vary across the landscape. Even within the same geographic region, lakes and streams in nutrient-poor watersheds are unproductive, oligotrophic, blue-water systems, while those nearby, containing numerous wetlands and forests, may be heterotrophic, stained, brown-water systems, and those in enriched watersheds are productive, autotrophic, green-water systems. This variation gives lakes and streams a wide range of potential responses. Not only do they signal environmental change at local scales, but also at regional to continental scales. For example, acidification of lakes and streams in the northeastern US is driven by mineral acids released into the atmosphere in the Midwest. Similarly, the Mississippi River transports nutrients, contaminants, and sediments from the northern edges of the US to the Gulf of Mexico (Figure 2). Watersheds provide a convenient unit with relatively well-defined boundaries to compare responses across the continent, and a common set of experimental approaches can be used to understand aquatic processes across diverse systems (Peterson *et al.* 2001; Webster *et al.* 2003).

■ Lake and stream metabolism can help us to understand climate-change impacts

Temperature

Climate change is complex, but one of the most fundamental metrics is temperature. Temperature controls many ecological processes, including ecosystem metabolism. Generally, an exponential increase in metabolic rates occurs with increasing temperature until inhibiting temperatures are reached (Brown *et al.* 2004). One of the best integrators of regional temperature is the timing of ice cover on lakes and rivers, because long-term records are available for this metric. A 1.2˚C warming of air temperatures in northern temperate regions has led to freeze dates that average 5.8 days later and ice-breakup dates that average 6.5 days earlier per 100 years (Magnuson *et al.* 2000). These temperature changes alter lake phenology in ways that may upset aquatic food webs by causing a mismatch between the seasonal timing of populations of primary consumers and their food resources (Winder and Schindler 2004). Reductions in ice cover also create a positive feedback mechanism that accelerates warming, due to the greater absorbance of solar radiation by open water in comparison to snow and ice. A connected network that provides continuous measurements of temperature, including the timing of ice cover, will provide us with a powerful metric of climate change and of ecosystem function at regional scales.

Carbon cycling

Understanding the fate of organic carbon in aquatic ecosystems is central to understanding the dynamics of climate change. Terrestrial carbon enters streams and is altered and transported by streams. Some carbon is metabolized (respired or altered chemically), additional carbon may be added by photosynthetic organisms, and some may be deposited in stream and river sediments (Hall 1995; Mulholland 1992). Streams move both organic and inorganic carbon into lakes, where there is substantial additional processing. Although lakes and reservoirs comprise less than 2% of the surface area of the planet, more organic carbon is deposited in their sediments than in the world's oceans (Dean and Gorham 1998) and lakes receive about twice as much terrestrially derived C as do the oceans (Cole *et al.* 2007). The terrestrial subsidies of organic carbon make most lakes net heterotrophic: ecosystem respiration exceeds gross primary production and, as a result, these lakes release more CO_2 to the atmosphere than they consume (Cole *et al.* 1994). Most organic carbon in the water column of lakes and streams is in the form of dissolved organic carbon (DOC). In lakes, DOC influences metabolism by decreasing water transparency and reducing the amount of sunlight available for photosynthesis, as well as altering thermal structure by decreasing the mixing depth. DOC provides a source of fixed carbon for microbial food webs, driving microbial respiration and fermentation in lakes and streams. DOC also absorbs potentially damaging UV radiation, resulting in photobleaching and release of more bio-

Table 1. Examples of sentinel responses of lakes and streams to three primary environmental forcings

Environmental forcings	*Sentinel response variables*	
Climate	***Specific responses***	***Responses to all three forcings***
Temperature	Period of ice cover Mixing of depth (L)	Water transparency (ultraviolet radiation [UVR], photosynthetically active radiation [PAR])
Precipitation	Water level	
		Temperature
Land use		
Erosion	Suspended solids Sedimentation rates (L)	Oxygen profiles
Nutrients	Nutrients (N, P, Si)	Conductivity, pH
Contaminants	Contaminants (PAH*, PCB**, atrazine)	DOC, DIC Algal pigments
Nitrogen deposition	Nitrogen concentrations	Chlorophyll (algal biomass) Phycocyanin (cyanobacteria)
	Nitrogen cycling rates	Paleolimnological (eg diatoms)
		Palynological (ie pollen)
		Indicators of anoxic metabolism (generation of methane and nitrous oxide)

Notes: Forcing is largely through the effects of the independent variables on terrestrial and atmospheric systems. In addition to the listed response variables, weather stations would monitor incident UVR, PAR, air temperature, relative humidity, and wind speed and direction. (L) = lakes only; (S) = streams only; * = polycyclic aromatic hydrocarbons; ** = polychlorinated biphenyls.

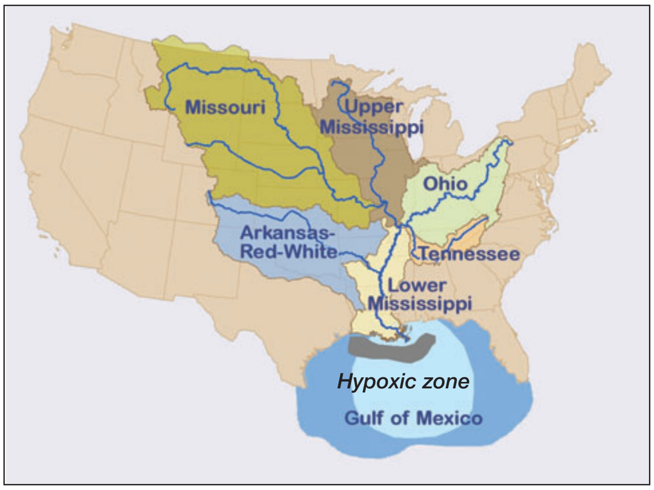

Figure 2. *Map showing how the Mississippi River interconnects the majority of states in the US. Continental-scale approaches to examine environmental impacts of this important river will require a network of monitoring and experimental sites, coordinated at the local (state), regional (major watershed basins shown), and continental (whole Mississippi River) scales.*

logically available carbon and CO_2. All of these processes connect terrestrial, atmospheric, and aquatic processes in ways that alter freshwater metabolism.

DOC concentrations in lakes and streams have changed dramatically in recent decades. Through the early 1990s, anthropogenic acidification and drought drove trends of decreasing DOC and increasing UV transparency in lakes in Europe and North America (Yan *et al.* 1996; Schindler *et al.* 1997). In recent years, even more striking increases in DOC have been observed in rivers draining peatlands (Freeman *et al.* 2004). DOC concentrations have doubled over the past 16 years in New York's Hudson River (Findlay 2005) and, in the past two decades, DOC has increased by an average of 91% in lakes and streams in the UK (Evans *et al.* 2006).

The prevailing hypothesis for recent increases in DOC in Europe and North America holds that human-dominated landscapes are beginning to recover from acidification following the passage of clean air legislation (Evans *et al.* 2006; Monteith *et al.* 2007). In contrast, more remote aquatic systems, such as those in the Yukon, have shown trends of decreasing DOC export that may signal destabilization of organic carbon stored in soils, potentially contributing to increased atmospheric CO_2 (Striegl *et al.* 2005). Human activities in riparian zones and immediate watersheds can also alter the carbon balance, nutrient inputs, and extent of heterotrophy through effects on the metabolism of lakes and streams (Carpenter *et al.* 1998b). Net biomass accumulation has ceased in forests of the northeastern US in recent decades (Likens 2004), but we do not know whether this is connected to observed trends in DOC. A continental- to global-scale observatory that monitors metabolism in lakes and streams and their connectivity with terrestrial systems is needed. Changes in dissolved oxygen, DOC, DIC, nutrients, and other variables can be used to address the causes and consequences of these widespread changes in terrestrially derived organic carbon (Table 1). Concurrent experimental manipulations of streams and lakes will allow us to better understand mechanisms that underlie the critical regulatory processes and thus mitigate problems ranging from acidification of inland waters to climate-change impacts.

■ Lake and stream metabolism can help us to understand land-use impacts

Land-use changes alter the metabolism of lakes and streams through the loading of sediments, nutrients, and contaminants, and can be measured in lakes with sediment traps. Anthropogenic loading of nitrogen and phosphorus to lakes and streams leads to eutrophication and degradation of water quality, including harmful algal blooms in coastal as well as inland waters (Smith *et al.* 2006). Nutrient loading can have considerable economic and ecological effects in freshwaters (Carpenter *et al.* 1998a; Dodds 2006a), one of the most serious being depletion of oxygen in deeper waters and the consequent development of "dead zones" in both lakes and coastal regions, often resulting in extensive fish kills (Dybas 2005).

While commonly used pesticides and herbicides may affect lake and stream metabolism through their effects on primary producers (Seguin *et al.* 2001), they also cause endocrine disruption in humans and wildlife. For example, atrazine, the most commonly used herbicide in the US, can induce sex changes in frogs at levels 30 times lower than EPA's safe drinking water standards, and 40 times below levels found in rainwater in agricultural regions of the US (Hayes *et al.* 2002). Thus, both streams and rainfall can transport these contaminants across the continent. Effects may be even more serious with exposure to multiple pesticides (Hayes *et al.* 2006). Water-borne pathogens, including the human protozoan parasites *Cryptosporidium parvii* and *Giardia lamblia*, are also widespread due to increased activity of humans, livestock, deer, geese, and other wildlife in the watersheds that drain into lakes and streams (Jellison *et al.* 2002; Brookes *et al.* 2004). Connectivity is thus provided not only by streams, but also by wildlife migration. Many of the receiving waters serve as municipal drinking water supplies. These toxic contaminants and pathogens may influence lake metabolism indirectly by altering primary production or the activities of consumers, including discouraging human recreational use and fishing.

Metabolism of lakes and streams is also altered by changes in the large regional- to continental-scale airsheds that deposit nutrients and contaminants to downwind areas (Likens and Bormann 1974). Atmospheric deposition can lead to nitrogen enrichment, acidification, and accumulation of mercury and toxic organic compounds. Atmospheric deposition of mercury derived from coal-burning power plants accumulates in aquatic food webs, leading to fish consumption advisories, such as those that have been implemented in most of the US

(Driscoll *et al.* 2007; Evers *et al.* 2007). One of the most insidious mechanisms of contamination is the "alpine distillery" – the atmospheric fractionation by which toxic compounds produced at low elevations are concentrated in seemingly pristine alpine lakes and streams (Figure 3). The toxicity of many of these contaminants may be mitigated by the presence of DOC (Oris *et al.* 1990; Weinstein and Oris 1999), but alpine lakes and streams are notoriously low in DOC due to the sparse vegetation within their watersheds. Atmospheric deposition further highlights the importance of landscape position in determining the effects of natural and human disturbances on inland waters (Kratz *et al.* 1997; Webster *et al.* 2000). For example, in Wisconsin, neighboring lakes sharing the same geological and climatic setting can differ substantially in size, color, and metabolism because of subtle differences in the lakes' positions in the local to regional hydrologic system. Lakes high in the flow system receive most of their water directly from the atmosphere, whereas those lower in the flow system receive additional water and solutes from streams or groundwater (Kratz *et al.* 2006).

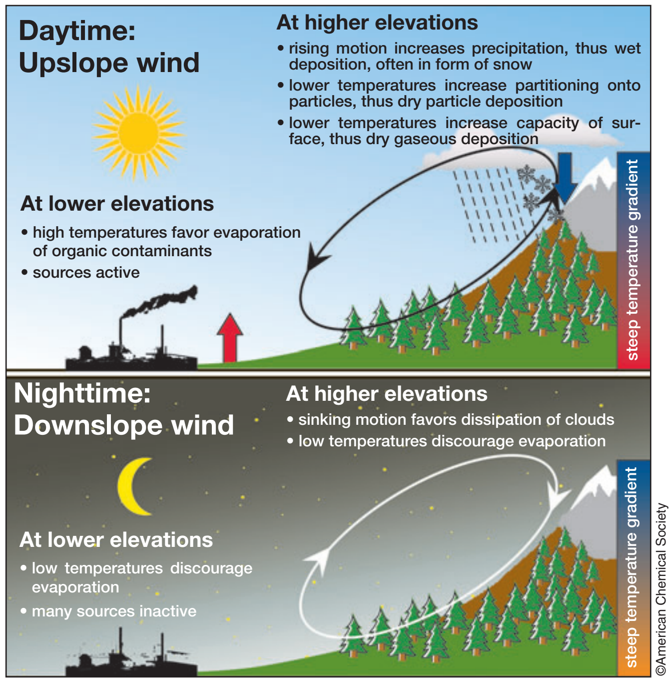

Figure 3. *The alpine distillery by which atmospheric fractionation concentrates contaminants in the pristine alpine lakes and streams that often provide drinking water supplies for major populations around the world. Modified with permission from Daly and Wania (2005).*

■ Lake and stream metabolism can help us to understand nitrogen deposition

Human activities have now more than doubled the input of fixed nitrogen to the world's ecosystems, with severe consequences for nutrient cycling, acidification, and biodiversity of terrestrial and aquatic ecosystems, as well as human health (Vitousek *et al.* 1997; Driscoll *et al.* 2003; Townsend *et al.* 2003). On a global basis, fixed nitrogen is one of the most important nutrients limiting primary productivity in both terrestrial and marine ecosystems, although phosphorus is often co-limiting (Vitousek *et al.* 1997; Elser *et al.* 2007). Heterotrophic metabolism is important in many freshwater systems (eg Dodds 2006a), and can also be limited by nitrogen (Tank and Dodds 2003). When nitrogen deposition exceeds about 7 kg ha^{-1}, some soils become saturated (Aber *et al.* 2003) and nitrogen is exported into streams, lakes, and coastal oceans. There is a direct correspondence between human population within a watershed and nitrogen output into rivers (Peierls *et al.* 1991). Lakes and streams are thus sentinels of nitrogen saturation in terrestrial systems, as well as important sites of nitrogen retention (Peterson *et al.* 2001), and can themselves become saturated with nitrogen (Bernot and Dodds 2005). Fertilization of experimental plots has shown that nitrogen deposition can stimulate increases in DOC export from soils to aquatic systems (Schmidt *et al.* 2004), and metabolic processing of DOC inputs in streams is tightly linked to nitrogen availability (Bernhardt and Likens 2002). Deposition of fixed nitrogen can also induce changes in diatom community structure in inland waters (Saros *et al.* 2005). The US Clean Air Act Amendments of 1990 have helped to reduce sulfate-induced acidification, but nitrogen deposition, which is less well regulated, continues to increase, and will likely replace sulfates as the primary source of anthropogenic acidification within the next decade (Likens 2004). Thus, measurements of nitrogen (and phosphorus), as well as DOC, pH, and dissolved oxygen, can provide information on N deposition-induced metabolic changes in lakes and streams (Table 1).

■ Connectivity between lakes, streams, and terrestrial ecosystems

Peters *et al.* (2008, in this issue) argue for integration of measurements and understanding of ecological connectivity over space and time. In all but the most xeric landscapes, lakes and streams are sentinels, providing a spatially connected framework that ties together the terrestrial landscape. Streams transport water and materials to and from the surrounding landscape, while the metabolism of lakes and streams integrates the consequent signals of environmental change over time. In contrast, migratory fish, such as salmon, can bring nutrients up from marine environments into rivers and other low-nutrient aquatic and terrestrial ecosystems at higher elevations (Naiman *et al.* 2002; Schindler *et al.* 2005). In addition to the integration and spatial connectivity provided by metabolic responses of these inland waters to changes in climate, land use, and nitrogen deposition, lakes provide integration and connectivity over longer time periods, through signals deposited in their sediments, such as shifts in tree pollen, diatom frustules, and organic carbon content (Table 1). The extensive connectivity of lakes and streams also provides a conduit for

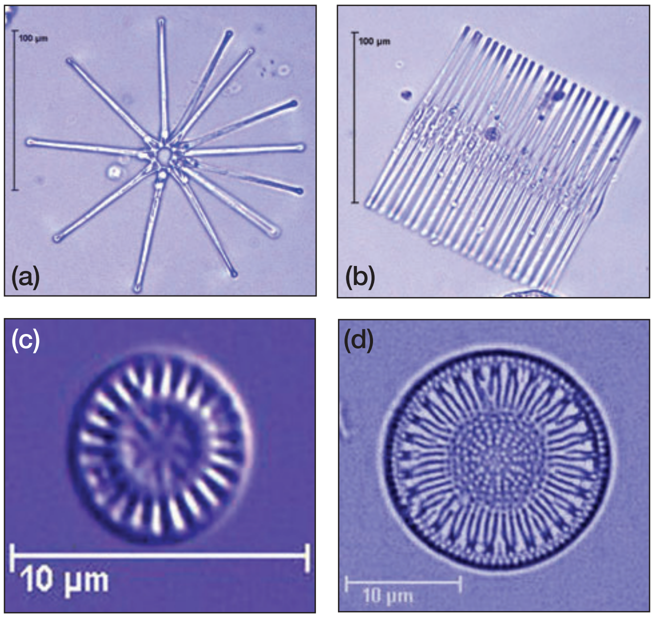

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Figure 4. *Diatoms are microscopic algae that serve as primary producers and food for consumers in many lakes and streams. Diatoms also provide signals of environmental change, through the silica cell walls (frustules) they leave behind after they die, in the sediments of lakes. With their differential sensitivity to environmental change, diatom species present in sediments help scientists to estimate historical changes in a wide range of environmental conditions, including acidification, temperature, and drought. Time intervals that can be resolved range from as short as a decade to thousands of years. For example, (a)* Asterionella formosa *and (b)* Fragilaria crotonensis *are increasing in abundance in alpine lakes, due to increases in nitrogen deposition. (c)* Discostella stelligera *and (d)* Cyclotella bodanica *have shown rapid changes in abundance in the sediments of alpine and Arctic lakes for as yet unexplained reasons. Combining such paleolimnological records with palynological (pollen) records permits us to extend the timeline of our understanding of environmental change in not only lakes and streams, but in terrestrial ecosystems as well.*

both waterborne pathogens and invasive exotic species to enter the landscape, with consequences that translate to costs in billions of dollars per year (Crowl *et al.* [2008] in this issue).

Peters *et al.* (2008, in this issue) also emphasize the need for making connections between short- and long-term dynamics, as well as for a mechanistic level of understanding to enable the prediction of future conditions never before experienced in Earth's history. This requires linking experimental and modeling approaches with long-term dynamics, as assessed by a spatially connected network. Lakes and streams have particularly well-defined boundaries and their metabolism is usually driven by populations of microscopic organisms with very short generation times. These characteristics make freshwater systems unusually responsive to environmental change and amenable to experimental manipulation. When short-term ecological experiments and long-term paleoecological and palynological (pollen) records are used in concert, inland waters can link ecosystem dynamics across time scales ranging from days to millennia and simultaneously elucidate the mechanisms of change (Saros *et al.* 2003, 2005; Figure 4). These long-term records provide critical information on the resistance and resilience of ecosystems to human-induced change.

Table 2. Questions and hypotheses for two complementary approaches to using lakes and streams as sentinels and integrators of changes in response to the three primary environmental forcing variables: climate, land use, and nitrogen deposition

Question	*Core hypotheses*
Based on interaction scales: How will chronic nutrient inputs (N or P), higher probabilities of extreme events (eg droughts and floods), and simplification of food webs (eg loss of consumers) impact the resistance and resilience of metabolism, nutrient cycling, and nutrient retention by lakes and streams?	**H1: Resistance and resilience of ecosystem functioning** Productivity, respiration, nutrient cycling, and retention are jointly determined by frequency of extreme hydrologic events (droughts, floods), rate of nutrient loading, and food web structure.
	H2: Time scales of ecosystem feedbacks and regime shifts Long-term nutrient loading and increased frequency of hydrological disturbance interact to promote irreversible "regime" shifts that alter resistance and resilience of ecosystem function to droughts and floods (hydrologic disturbance).
	H3: Spatial scales of response Resilience and recovery of ecosystem functioning over large (continental) scales will vary with regional context, including local species composition and diversity, climate, and hydrological disturbance regime.
Based on environmental forcing: How do changes in climate, land use, and invasive species alter lake and stream metabolism and, consequently, ecosystem services, through biogeochemical, biodiversity, and hydro-ecological responses?	**H1: Climate change** Alters ecosystem metabolism and phenology by altering organic matter loading in lakes and streams, as well as the thermal structure and extent of anoxia in lakes.
	H2: Changes in land use Alter ecosystem metabolism by changing nutrient, contaminant, sediment, and organic matter loading.
	H3: Invasive species Alter ecosystem metabolism by changing aquatic community structure and biomass and, hence, water transparency.

Where do we go from here?

Both observational and experimental approaches must be driven by core questions and hypotheses that can be addressed with common metrics across a wide variety of landscapes. We propose that lake and stream metabolism is a key metric (Table 2). To date there is little systematic, ongoing measurement of aquatic ecosystem metabolism across North America or any other continent. While this single ecosystem property is unlikely to provide information on subtle ecosystem effects, such as extinction of already rare species, sub-lethal toxic effects, and alterations in community structure, it is the most basic measurement of ecosystem function. Strong continental gradients in precipitation, temperature, nitrogen deposition, and human land-use patterns (Peters *et al.* [2008] in this issue) will guide the design of observational work. Long-term, networked sites located strategically across these gradients can be used to assess the responses of lake and stream metabolism and to monitor transport of contaminants, pathogens, and invasive species (Crowl *et al.* [2008] in this issue). Episodic weather events, including hurricanes, floods, and droughts will provide "natural experiments" to help tease out the causes and consequences of change.

Conclusions

Lakes and streams are key sentinels and integrators of environmental change in the surrounding terrestrial landscape. In addition to providing water for drinking, bathing, recreation, and commercial and industrial use, inland waters provide many other ecosystem services to both humans and wildlife. Lakes and streams are the arteries and veins of the surrounding landscape. While current, long-term monitoring programs have provided key insights that would not otherwise have been possible (Lovett *et al.* 2007), they are not in and of themselves adequate for the task at hand. A more sophisticated and interconnected continental-scale network is essential to address the rapid, large-scale environmental changes that we are experiencing across the planet.

Acknowledgements

The authors thank the many members of the Global Lakes Ecological Observatory Network (GLEON) and the Stream Ecological Observatory Network (STREON), particularly B Cardinale, M Whiles, N Grimm, S Hamilton, and S Johnson, who have contributed to the development of the ideas behind this manuscript through their responses to the National Ecological Observatory Network request for information (NEON RFI). This work was supported by NSF IRCEB 0210972, NSF DEB-0639901, NSF EPSCoR 0553722, NSF DBI-0439384, NSF DEB-0217533, NSF DBI-0639229, and the Gordon and Betty Moore Foundation. This is Contribution Number 4145 of the University of Maryland Center for Environmental Science. We thank the NSF LTER program for its support.

References

Aber JD, Goodale CL, Ollinger SV, *et al.* 2003. Is nitrogen deposition altering the nitrogen status of northeastern forests? *BioScience* **53**: 375–89.

Bernhardt ES and Likens GE. 2002. Dissolved organic carbon enrichment alters nitrogen dynamics in a forest stream. *Ecology* **83**: 1689–1700.

Bernot MJ and Dodds WK. 2005. Nitrogen retention, removal, and saturation in lotic ecosystems. *Ecosystems* **8**: 442–53.

Brookes JD, Antenucci J, Hipsey M, *et al.* 2004. Fate and transport of pathogens in lakes and reservoirs. *Environ Int* **30**: 741–59.

Brown JH, Gillooly JF, Allen AP, *et al.* 2004. Toward a metabolic theory of ecology. *Ecology* **85**: 1771–89.

Carpenter SR, Bolgrien D, Lathrop RC, *et al.* 1998a. Ecological and economic analysis of lake eutrophication by nonpoint pollution. *Aust J Ecol* **23**: 68–79.

Carpenter SR, Cole JJ, Kitchell JF, and Pace ML. 1998b. Impact of dissolved organic carbon, phosphorus, and grazing on phytoplankton biomass and production in experimental lakes. *Limnol Oceanogr* **43**: 73–80.

Cole JJ, Prairie Y, Caraco N, *et al.* 2007. Plumbing the global carbon cycle: integrating inland waters into the terrestrial carbon budget. *Ecosystems* **10**: 171–84.

Cole JJ, Caraco NF, Kling GW, and Kratz TK. 1994. Carbon dioxide supersaturation in the surface waters of lakes. *Science* **265**: 1568–70.

Cole JJ, Carpenter SR, Pace ML, *et al.* 2006. Differential support of lake food webs by three types of terrestrial organic carbon. *Ecol Lett* **9**: 558–68.

Crowl T, Crist T, Parmenter R, *et al.* 2008. The spread of invasive species and infectious disease as drivers of ecosystem change in an increasingly connected world. *Front Ecol Environ* **6**: 238–246.

Daly GL and Wania F. 2005. Organic contaminants in mountains. *Environ Sci Technol* **39**: 385–98.

Dean WE and Gorham E. 1998. Magnitude and significance of carbon burial in lakes, reservoirs, and peatlands. *Geology* **26**: 535–38.

Dodds WK. 2002. Freshwater ecology: concepts and environmental applications. New York, NY: Academic Press.

Dodds WK. 2006a. Eutrophication and trophic state in rivers and streams. *Limnol Oceanogr* **51**: 671–80.

Dodds WK. 2006b. Nutrients and the "dead zone": ecological stoichiometry and depressed dissolved oxygen in the northern Gulf of Mexico. *Front Ecol Environ* **4**: 211–17.

Driscoll CT, Evers DC, Lambert KF, *et al.* 2007. Mercury matters: linking mercury science with public policy in the northeastern United States. www.hubbardbrookfoundation.org/article/view/13188/1/2076. Viewed 13 Mar 2007.

Driscoll CT, Whitall D, Aber J, *et al.* 2003. Nitrogen pollution in the northeastern United States: sources, effects, and management options. *BioScience* **53**: 357–74.

Dybas CL. 2005. Dead zones spreading in world oceans. *BioScience* **55**: 552–57.

Elser JJ, Bracken MES, Cleland EE, *et al* 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecol Lett* **10**: 1135–42.

Evans CD, Chapman PJ, Clark JM, *et al.* 2006. Alternative explanations for rising dissolved organic carbon export from organic soils. *Glob Change Biol* **12**: 2044–53.

Evers DC, Han YJ, Driscoll CT, *et al.* 2007. Biological mercury hotspots in the northeastern United States and southeastern Canada. *BioScience* **57**: 29–43.

Findlay SEG. 2005. Increased carbon transport in the Hudson River: unexpected consequence of nitrogen deposition? *Front Ecol Environ* **3**: 133–37.

Freeman C, Fenner N, Ostle NJ, *et al.* 2004. Export of dissolved organic carbon from peatlands under elevated carbon dioxide levels. *Nature* **430**: 195–98.

Hall RO. 1995. Use of a stable carbon isotope addition to trace bacterial carbon through a stream food web. *J N Am Benthol Soc* **14**: 269–78.

Hanson PC, Bade DL, Carpenter SR, and Kratz TK. 2003. Lake metabolism: relationships with dissolved organic carbon and phosphorus. *Limnol Oceanogr* **48**: 1112–19.

Hayes T, Case P, Chui S, *et al.* 2006. Pesticide mixtures, endocrine disruption, and amphibian declines: are we underestimating the impact? *Environ Health Persp* **114 S1**: 40–50.

Hayes T, Haston K, Tsui M, *et al.* 2002. Feminization of male frogs in the wild. *Nature* **419**: 895–96.

Huq A, Small EB, West PA, *et al.* 1983. Ecological relationships between *Vibrio cholerae* and planktonic crustacean copepods. *Appl Environ Microb* **45**: 275–83.

Jellison KL, Hemond HF, and Schauer DB. 2002. Sources and species of *Cryptosporidium* oocysts in the Wachusett Reservoir watershed. *Appl Environ Microb* **68**: 569–75.

Jenkins M. 2003. Prospects for biodiversity. *Science* **302**: 1175–77.

Johannessen OM, Shalina EV, and Miles MW. 1999. Satellite evidence for an Arctic Sea ice cover in transformation. *Science* **286**: 1937–39.

Kratz TK, Webster KE, Bowser CJ, *et al.* 1997. The influence of landscape position on lakes in northern Wisconsin. *Freshwater Biol* **37**: 209–17.

Kratz TK, Webster KE, Riera JL, *et al.* 2006. Making sense of the landscape: geomorphic legacies and the landscape position of lakes. In: Magnuson JJ, Kratz TK, and Benson BJ (Eds). Long-term dynamics of lakes in the landscape: long-term ecological research on north temperate lakes. New York, NY: Oxford University Press.

Likens GE. 2004. Some perspectives on long-term biogeochemical research from the Hubbard Brook Ecosystem study. *Ecology* **85**: 2355–62.

Likens GE and Bormann FH. 1974. Linkages between terrestrial and aquatic ecosystems. *BioScience* **24**: 447–56.

Lovett GM, Burns DA, Driscoll CT, *et al.* 2007. Who needs environmental monitoring? *Front Ecol Environ* **5**: 253–60.

Magnuson JJ, Robertson DM, Benson BJ, *et al.* 2000. Historical trends in lake and river ice cover in the northern hemisphere. *Science* **289**: 1743–46.

Monteith DT, Stoddard JL, Evans CD, *et al.* 2007. Dissolved organic carbon trends resulting from changes in atmospheric deposition chemistry. *Nature* **450**: 537–41.

Mulholland PJ. 1992. Regulation of nutrient concentrations in a temperate forest stream: roles of upland, riparian, and instream processes. *Limnol Oceanogr* **37**: 1512–26.

Naiman RJ, Bilby RE, Schindler DE, and Helfield JM. 2002. Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. *Ecosystems* **5**: 399–417.

Oris JT, Hall AT, and Tylka JD. 1990. Humic acids reduce the photo-induced toxicity of anthracene to fish and *Daphnia*. *Environ Toxicol Chem* **9**: 575–83.

Peierls BJ, Caraco NF, Pace ML, and Cole JJ. 1991. Human influence on river nitrogen. *Nature* **350**: 386–87.

Peters DPC, Groffman PM, Nadelhoffer KJ, *et al.* 2008. Living in an increasingly connected world: a framework for continental-scale environmental science. *Front Ecol Environ* **6**: 229–237.

Peterson BJ, Wollheim WF, Mulholland PJ, *et al.* 2001. Control of nitrogen export from watersheds by headwater streams. *Science* **292**: 86–90.

Poff NL, Brinson MM, and Day JW. 2002. Aquatic ecosystems and global climate change: potential impacts on inland freshwater and coastal wetland ecosystems in the United States. www.pewtrusts.org/our_work_ektid30677.aspx. Viewed 9 Aug 2007.

Ricciardi A and Rasmussen JB. 1999. Extinction rates of North American freshwater fauna. *Conserv Biol* **13**: 1220–22.

Roberts BJ, Mulholland PJ, and Hill WR. 2007. Multiple scales of temporal variability in ecosystem metabolism rates: results from 2 years of continuous monitoring in a forested headwater stream. *Ecosystems* **10**: 588–606.

Rose JB, Gerba CP, and Jakubowski W. 1991. Survey of potable water-supplies for *Cryptosporidium* and *Giardia*. *Environ Sci Technol* **25**: 1393–1400.

Saros JE, Interlandi S, Wolfe AP, and Engstrom DR. 2003. Recent changes in the diatom community structure of lakes in the Beartooth Mountain Range, USA. *Arct Antarct Alp Res* **35**: 18–23.

Saros JE, Michel TJ, Interlandi S, and Wolfe AP. 2005. Resource requirements of *Asterionella formosa* and *Fragilaria crotonensis* in oligotrophic alpine lakes: implications for recent phytoplankton community reorganizations. *Can J Fish Aquat Sci* **62**: 1681–89.

Schindler DE, Leavitt PR, Brock CS, *et al.* 2005. Marine-derived nutrients, commercial fisheries, and production of salmon and lake algae in Alaska. *Ecology* **86**: 3225–31.

Schindler DW, Curtis PJ, Bayley SE, *et al.* 1997. Climate-induced changes in the dissolved organic carbon budget of boreal lakes. *Biogeochemistry* **36**: 9–28.

Schmidt SK, Lipson DA, Ley RE, *et al.* 2004. Impacts of chronic nitrogen additions vary seasonally and by microbial functional group in tundra soils. *Biogeochemistry* **69**: 1–17.

Seguin F, Leboulanger C, Rimet F, *et al.* 2001. Effects of atrazine and nicosulfuron on phytoplankton in systems of increasing complexity. *Arch Environ Con Tox* **40**: 198–208.

Smith VH, Joye SB, and Howarth RW. 2006. Eutrophication of freshwater and marine ecosystems. *Limnol Oceanogr* **51**: 351–55.

Striegl RG, Aiken GR, Dornblaser MM, *et al.* 2005. A decrease in discharge-normalized DOC export by the Yukon River during summer through autumn. *Geophys Res Lett* **32**: L21413.

Tank J and Dodds WK. 2003. Responses of heterotrophic and autotrophic biofilms to nutrients in ten streams. *Freshwater Biol* **48**: 1031–49.

Townsend AR, Howarth RW, Bazzaz FA, *et al.* 2003. Human health effects of a changing global nitrogen cycle. *Front Ecol Environ* **1**: 240–46.

US EPA (Environmental Protection Agency). 2003. Analysis and findings of the Gallup organization's drinking water customer satisfaction survey. Washington, DC: US Environmental Protection Agency Office of Groundwater and Drinking Water. EPA 816-K-03-005.

Vitousek PM, Aber JA, Howarth RW, *et al.* 1997. Human alteration of the global nitrogen cycle: sources and consequences. *Ecol Appl* **7**: 737–50.

Webster JR, Mulholland PJ, Tank JL, *et al.* 2003. Factors affecting ammonium uptake in streams – an inter-biome perspective. *Freshwater Biol* **48**: 1329–52.

Webster KE, Newell AD, Baker LA, and Brezonik PL. 2000. Climatically induced rapid acidification of a softwater seepage lake. *Nature* **347**: 374–76.

Weinstein JE and Oris JT. 1999. Humic acids reduce the bioaccumulation and photoinduced toxicity of fluoranthene in fish. *Environ Toxicol Chem* **18**: 2087–94.

Winder M and Schindler DE. 2004. Climate change uncouples trophic interactions in an aquatic ecosystem. *Ecology* **85**: 2100–06.

Yan ND, Keller W, Scully NM, *et al.* 1996. Increased UV-B penetration in a lake owing to drought-induced acidification. *Nature* **381**: 141–43.

