

Climate Change and the World's “Sacred Sea”—Lake Baikal, Siberia

MARIANNE V. MOORE, STEPHANIE E. HAMPTON, LYUBOV R. IZMEST'EVA, EUGENE A. SILOW,
EKATERINA V. PESHKOVA, AND BORIS K. PAVLOV

Lake Baikal—the world's largest, oldest, and most biotically diverse lake—is responding strongly to climate change, according to recent analyses of water temperature and ice cover. By the end of this century, the climate of the Baikal region will be warmer and wetter, particularly in winter. As the climate changes, ice cover and transparency, water temperature, wind dynamics and mixing, and nutrient levels are the key abiotic variables that will shift, thus eliciting many biotic responses. Among the abiotic variables, changes in ice cover will quite likely alter food-web structure and function most because of the diverse ways in which ice affects the lake's dominant primary producers (endemic diatoms), the top predator (the world's only freshwater seal), and other abiotic variables. Melting permafrost will probably exacerbate the effects of additional anthropogenic stressors (industrial pollution and cultural eutrophication) and could greatly affect ecosystem functioning.

Keywords: Lake Baikal, climate change, ice dynamics, anthropogenic stressors, synergistic effects

Lake Baikal in southeastern Siberia, the “Sacred Sea,” incites strong emotions and action in Russia. In March 2006, 5000 people in Irkutsk, Russia, protested the proposed construction of an oil pipeline scheduled to pass within 800 meters (m) of Lake Baikal's shoreline, and, within days, President Putin announced the pipeline would be rerouted outside the lake's watershed (Cullison 2007). In July 2007, environmental activists protested against the expansion of an uranium enrichment plant in Angarsk, Russia, located within the airshed of Lake Baikal; one protester was killed and several were seriously injured by young men allegedly hired by regional authorities who favor expansion of the plant (Cullison 2007).

Russians are strongly attached emotionally to Lake Baikal, in part because it represents the natural unspoiled beauty of the Russian motherland. Indeed, this natural phenomenon was the birthplace of the Russian environmental movement in the mid-1960s (Weiner 1999), a movement that endures today.

Lake Baikal is a treasure trove for biologists. In part because of its great antiquity (it is approximately 25 million years old) and its deep, oxygenated water, this lake harbors more species than any other lake in the world, and many of them are endemic (Martin 1994). More than half of the approximately 2500 animal species (Timoshkin 1995) and 30% of the 1000

plant species are endemic (Bondarenko et al. 2006a); 40% of the lake's species are still undescribed (Timoshkin 1995). The presence of oxygen down to its deepest depths (1642 m), a trait shared with the ocean but unique among deep lakes (> 800 m), explains the presence of multicellular life and the evolution of an extensive, mostly endemic fauna in the lake's profundal depths. For example, hydrothermal vent communities dependent on access to oxygen for chemoautotrophy occur on the lake floor (Crane et al. 1991). In recognition of its biodiversity and endemism, UNESCO (United Nations Educational, Scientific and Cultural Organization) declared Lake Baikal a World Heritage site in 1996. The lake's biotic richness is matched by physical distinctions: it is the largest lake in the world by depth and volume. Reaching oceanic depths, Lake Baikal holds 20% of Earth's liquid freshwater (equivalent to all of the North American Great Lakes combined).

Unfortunately, multiple and diverse anthropogenic stressors threaten this extraordinary lake, as the recent protests in Siberia illustrate. Among these stressors, climate change is arguably the most insidious because of its seemingly inexorable momentum and the many ways in which it can create synergisms with other anthropogenic stressors currently confronting the lake. In this article, we (a) describe contemporary climate change in the Lake Baikal region and future climate

projections for this part of the world; (b) illustrate the potential ecological effects of climate change, while highlighting how these effects differ from those in other lakes (e.g., Smol and Douglas 2007); and (c) discuss synergistic effects between climate change and other anthropogenic stressors that are particularly important for the Sacred Sea. This article builds on recent climate-change projections for the Baikal diatom community (Mackay et al. 2006) by discussing the potential responses of all pelagic trophic levels, physical mixing processes, and synergisms with other anthropogenic stressors.

Evidence of climate change

Located in southeastern Siberia (figure 1), Lake Baikal is adjacent to the Central Siberian Plateau, one of three areas in the world experiencing the most rapid climate change; the other two regions are the Antarctic Peninsula and northwestern North America (Clarke et al. 2007). All three areas are distinguished by long, cold winters. For example, winter air temperatures at Lake Baikal reach -37 degrees Celsius ($^{\circ}\text{C}$) to -40°C , and the lake freezes for four to five months each year;

summer air temperatures soar briefly to 25°C to 30°C in this strongly continental climate (Kozhova and Izmes't'eva 1998). Spatial variation in precipitation is high across the watershed, with the western coast receiving about 400 millimeters (mm) of precipitation annually, while as much as 600 to 800 mm are deposited on the southeastern coast (Shimaraev et al. 1994).

Evidence of rapid climate change in the Baikal region is now abundant (figure 2). Annual air temperatures increased 1.2°C over the last century—twice the global average—with winter temperatures increasing more (2°C) than those in summer (0.8°C) (Shimaraev et al. 2002). Furthermore, surface waters of Lake Baikal warmed rapidly and significantly to a depth of 25 m during the last 60 years (Hampton et al. 2008). In addition, the ice-free season lengthened 18 days from 1869 to 2000, and ice thickness decreased 12 centimeters (cm) between 1949 and 2000 in the southern basin (Shimaraev et al. 2002). As air temperatures warmed, annual precipitation and snow depth increased 0.59 mm per year (83 to 130 mm) and 0.135 cm per year (24 to 30 cm), respectively, over northern Eurasia between 1936 and 1995 (Kitaev et al.

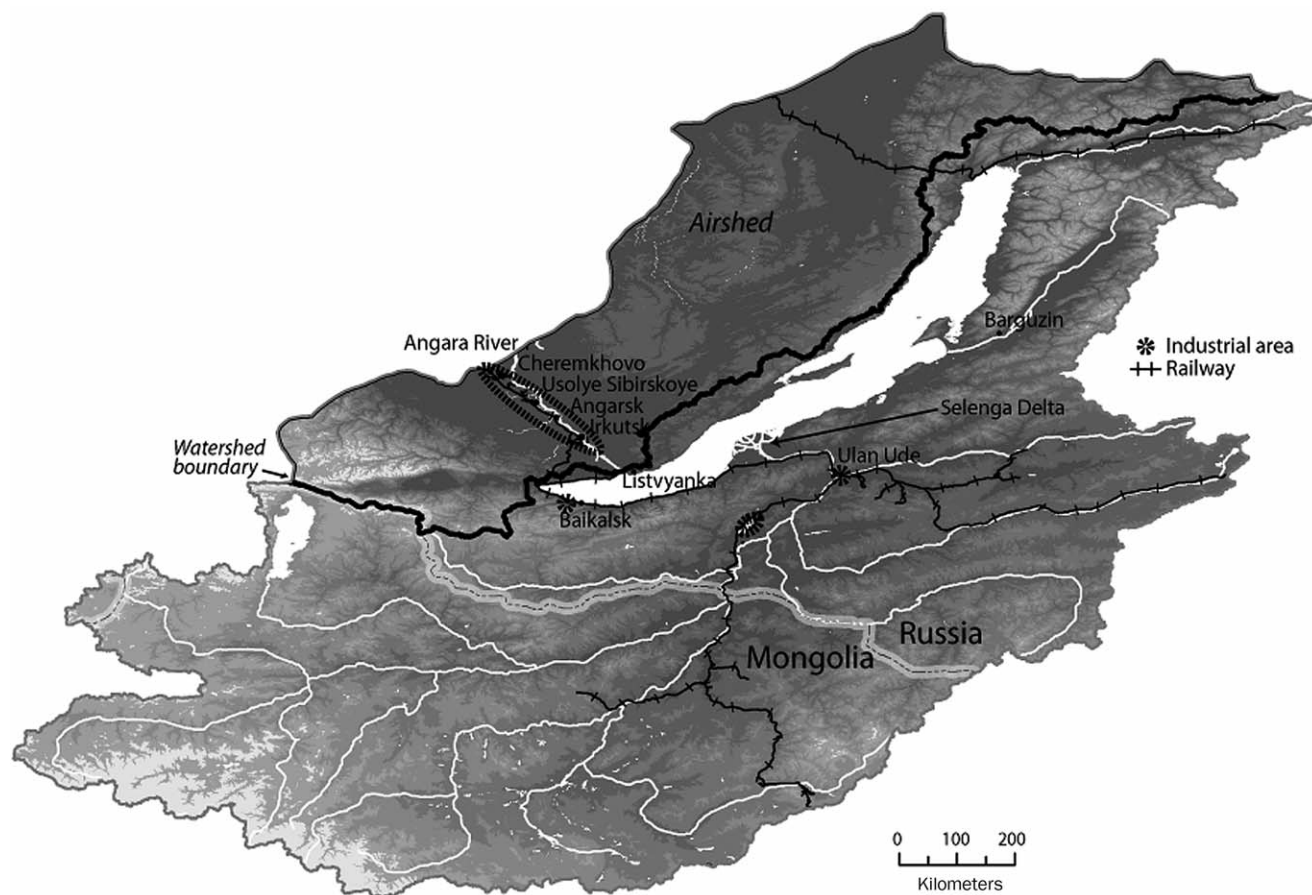


Figure 1. Lake Baikal, the largest (by depth and volume), oldest, and most biotically rich lake on Earth, is located at a subarctic latitude (52°N to 56°N latitude) within southeastern Siberia. The lake's watershed, situated within Russia and Mongolia, lies mostly to the east and south of the lake while the airshed extends west of the lake to include an industrial corridor (delineated by a black oval) along the Angara River, the sole river draining the lake. The Trans-Siberian railroad bisects this corridor, continuing around the southern end of the lake, and a large pulp mill built in the late 1960s is located in the town of Baikalsk. The Selenga River, draining much of Mongolia, is the lake's major tributary, delivering more than 50% of the lake's surface inflow.

2002). Concomitantly, river inflow into Lake Baikal increased significantly, by 300 m³ per second (0.4% of total river inputs), during the last century (Shimaraev et al. 2002).

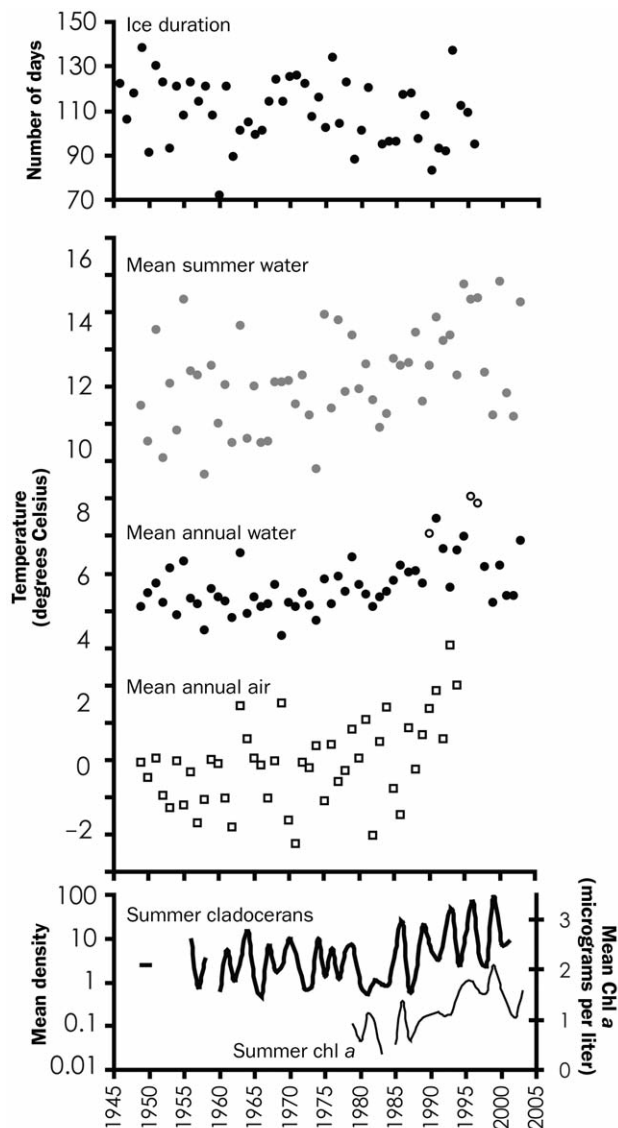


Figure 2. Long-term trends in winter ice duration (data from Benson and Magnuson 2000); air temperature (data from NOAA 1994); water surface temperature, density of cladocerans (individuals per liter), and summer mean chlorophyll a (chl a; Izmet'eva 2006) at or near Lake Baikal, Siberia. The trend in winter ice duration is highly significant for the period 1869–2000 (Shimaraev et al. 2002, Todd and Mackay 2003), but only data for 1945–1996 are shown here. Three annual average water temperature values were missing two or more winter months of data, and these points are noted as hollow circles. Air temperature data are from the city of Irkutsk, ending in 1994. Summer values are averages for July, August, and September, the months in which stratification can occur.

Projected climate change

Climatic changes of the past century are likely to intensify in the Baikal region, becoming warmer and wetter by the latter part of the 21st century, particularly during winter months (December, January, and February) (table 1; Christensen et al. 2007). According to climate projections for the Baikal region (Northern Asia, 50–70°N, 40–180°E) in Christensen and colleagues (2007), by the years 2080–2099, annual air temperatures will have increased by a median of 4.3°C relative to average temperatures of 1980–1999, with greater warming expected in winter (6.0°C = median projected increase for winter months) than in summer (3.0°C = median projected increase for June, July, and August). Air temperature increases of a similar magnitude are projected for Alaska, the Arctic, Greenland, and Iceland (Christensen et al. 2007).

Median winter precipitation is expected to increase by 26% (12% to 55% = minimum to maximum) by the end of the 21st century (table 1; Christensen et al. 2007). Only one other region of the world—the Arctic—is predicted to exceed the increase in frequency of “wet” winters projected for the Baikal region. The projected increase in summer precipitation (i.e., median = 9%) is one-third of that projected for winter (table 1). Importantly, more precipitation may fall as rain than as snow, influencing ice transparency, during the spring months (March, April, and May) of some years when air temperatures, currently averaging -5.0°C (Shimaraev et al. 1994), rise above freezing.

Projections of changes in wind dynamics (speed, direction, frequency) do not yet exist, but as local differences in atmospheric pressure between land and water grow, it is likely that warming will generate greater wind activity (Shimaraev et al. 1994). Enhanced wind activity is particularly important for large lakes that already experience augmented wind fetch (i.e., wind speed increases by a factor of two or more for moderate winds over large bodies of water), as compared with land or small lakes with shoreline sheltering.

Response to climate change

A variety of abiotic drivers strongly influence ecosystem processes in Lake Baikal, and the magnitude of their responses to climate change will largely determine how this lake functions in the late 21st century. Key drivers include ice duration and transparency, water temperature, wind and mixing dynamics, and nutrient loading (figure 3).

Ice duration and transparency. Unlike the case with many lakes in the world, ice is arguably the single most important abiotic driver in Lake Baikal, because the lake's dominant primary producers and its top predator require ice for population growth (box 1). In temperate-zone lakes, the spring phytoplankton bloom begins shortly after ice off (when the last ice breakup before summer's open waters is observed); but in Lake Baikal, the spring bloom occurs under the ice, and ice is essential for initiating and sustaining this bloom (figure 4). Large endemic diatoms (e.g., *Aulacoseira baicalensis*) frequently dominate the bloom, living and reproducing within

Table 1. Regional projections of increases in temperature and precipitation for the years 2080–2099 from 21 global models for the Baikal portion of Asia (Northern Asia, 50–70°N, 40–180°E).

Season	Temperature increase (°C)			Precipitation increase (percentage)			Extreme seasons (percentage)		
	Minimum	Median	Maximum	Minimum	Median	Maximum	Warm	Wet	Dry
DJF	2.9	6.0	8.7	12	26	55	93	68	0
MAM	2.0	3.7	6.8	2	18	26	89	66	1
JJA	2.0	3.0	5.6	–1	9	16	100	51	2
SON	2.8	4.8	6.9	7	17	29	99	65	0
Annual	2.7	4.3	6.4	10	15	25	100	92	0

DJF, December, January, February; MAM, March, April, May; JJA, June, July, August; SON, September, October, November.

Note: Projections are for the 2080–2099 period, in comparison with model runs for the 1980–1999 period. Minimum, maximum, and median values for temperature (degrees Celsius) increase and percentage precipitation change are shown. Frequency (percentage) of extremely warm, wet, or dry seasons, averaged over all models, is defined as the frequency of years in which temperature (precipitation) values exceeded those for the warmest (wettest or driest) 5% of all winters, summers, falls, and springs during the 1980–1999 control period.

Source: IPCC (2007) and Christensen and colleagues (2007).

the interstitial spaces of the ice (Obolkin et al. 2000) and forming filaments more than 10 cm in length that hang from the ice into the water below. When currents dislodge the diatom filaments in the littoral zone, the filaments aggregate and form large flakes that sink and cover the substrate. Here the mucopolysaccharide coating of the flakes and filaments

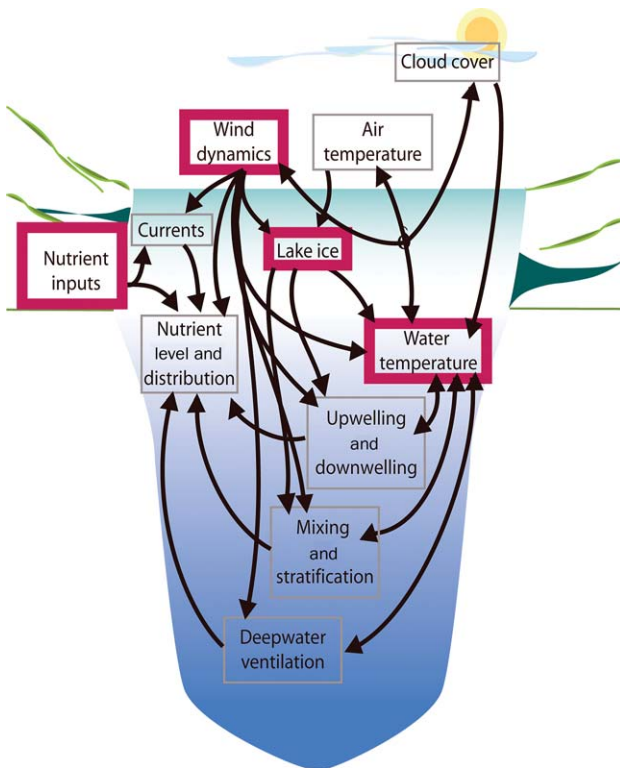


Figure 3. Conceptual diagram showing key abiotic drivers in maroon rectangles (i.e., lake ice, water temperature, wind and mixing, and nutrient loading) that will both respond to climate change and very likely force the greatest change in biological processes in the Lake Baikal ecosystem, Siberia.

presumably provides an important food source for benthic animals, including gammarids and mollusks (Bondarenko et al. 2006b).

Climate change could threaten the under-ice algal bloom in Lake Baikal primarily through two mechanisms: shortening the period of ice cover and changing the ice transparency. Ice establishes the requisite abiotic conditions (convective mixing, dim light; figure 4) for growth of Baikal's endemic diatoms, and shortening the seasonal duration of ice could curtail or prevent the under-ice phytoplankton bloom. The duration of ice cover is predicted to shorten dramatically by the end of the 21st century, from at least two to four weeks (Todd and Mackay 2003), to possibly two months (Shimaraev et al. 2002). Recent experimental work in the Baltic Sea (Sommer and Lengfellner 2008) and empirical results from Lake Baikal (Izmet'seva et al. 2006) suggest the lake's endemic diatoms may continue blooming in April, as they currently do, rather than advancing their time of bloom formation to precede earlier ice-out dates of mid-April or earlier by the end of this century. Thus, the endemic diatoms could bloom when ice is absent and conditions for growth are unfavorable, because ice recession exposes them to stressfully high levels of irradiance at the water surface (Mackay et al. 2006) and promotes warming and stratification of surface waters, which adversely affect large heavy diatoms. Also, thinner ice has been observed already at Lake Baikal (Shimaraev et al. 2002), and this may reduce the under-ice convective mixing that suspends these large diatoms in the photic zone (figure 4; Granin et al. 2000). Therefore, reductions in both ice duration and ice thickness could adversely affect the primary productivity (PPR) of Lake Baikal's large endemic diatoms in early spring.

Changes in ice transparency—resulting in either more or less light penetration—could also alter the spring phytoplankton bloom, and several scenarios are possible with warmer, wetter winters. Global circulation models predict an increase in winter precipitation (table 1), which is likely to continue arriving as snow rather than as rain even in a warmer

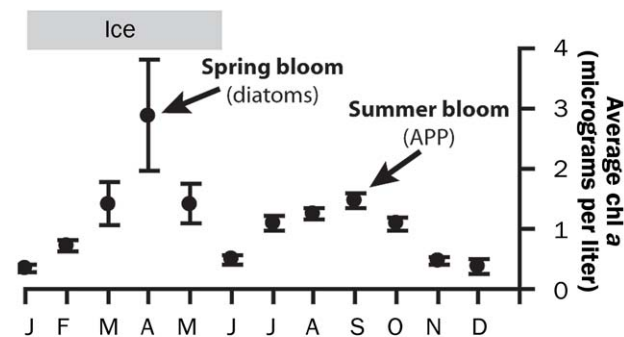


Figure 4. As in most temperate and subarctic lakes, two phytoplankton blooms occur each year in Lake Baikal, as indicated in this graph of mean (\pm one standard error) algal biomass, as measured by chlorophyll (chl a), versus month of the year. (Samples collected 2.7 kilometers off the southwestern shore every 7 to 10 days from 1979–2003; Hampton et al. 2008.) But, unlike many lakes, the larger spring bloom occurs under or within the transparent ice that is often free of snow over large portions of Lake Baikal, because strong winds sweep snow off the ice. Pelagic endemic diatoms, some of which are exceptionally large (1.5-centimeter filaments), flourish under the ice where sufficient solar radiation penetrates to power both photosynthesis and density-driven convective mixing, which keeps the heavy diatoms afloat under the ice (Granin et al. 2000). Vertical ice growth also promotes mixing, because as ice crystals form, ions are excluded, creating a layer of relatively high-density water under the ice that sinks and displaces additional water upward. The second phytoplankton bloom occurs in late summer–early fall when the upper water layer is warm and stratified, promoting the growth of bacteria-size (0.8 to 1.5 micrometers) autotrophic picoplankton (APP in the graph) and small cosmopolitan diatoms. Climate change will most likely favor these smaller algae over the large, cold-water endemic diatoms, with repercussions for both the pelagic and benthic food webs. Graph modified with permission from Hampton and colleagues (2008), © Wiley-Blackwell.

future, because temperatures in this region in the winter are far below freezing (Kozhova and Izmet'eva 1998). Previous work shows that when snow is deeper than 10 cm, low light levels inhibit photosynthesis and convective mixing weakens, causing heavy diatoms to sink out of the photic zone (Granin et al. 2000, Mackay et al. 2005). In fact, the relationship between snow depth and diatom assemblages is sufficiently robust that paleolimnologists have used the corrected relative abundance of Baikal diatom species in sediment cores to reconstruct historical snow depths as far back as 1000 years ago (Mackay et al. 2005). However, it is difficult to predict the effects of an increase in spring precipitation and a shift toward more rain rather than snow. Rain that falls on snow and re-freezes creates cloudy ice, although a great deal of rain may simply melt the snow and leave clear ice.

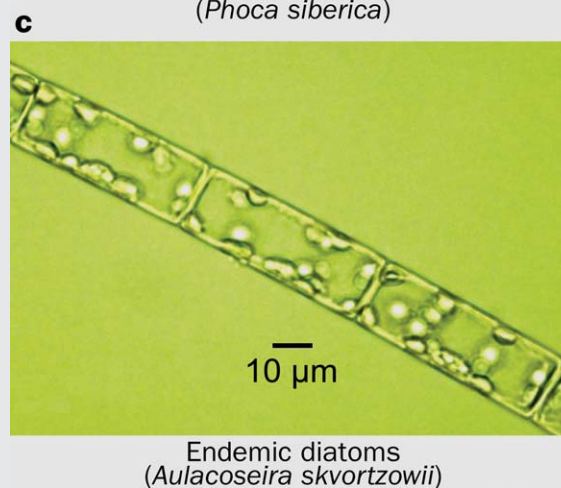
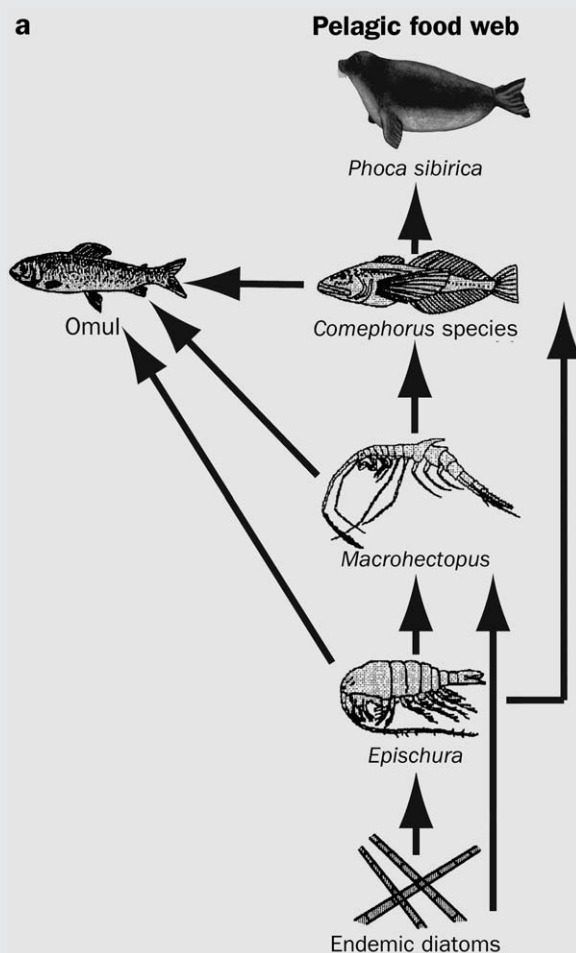
These proposed changes in ice transparency and in the duration of ice cover may shift the species composition of the spring phytoplankton community away from large endemic diatoms toward small cosmopolitan species that are opportunistic (e.g., *Synedra* spp., *Nitzschia*), a phenomenon observed in the sedimentary diatom record from the Medieval Warm Period (Bradbury et al. 1994, Mackay et al. 2005). The resulting shift in algal size distribution, in combination with a reduction in the magnitude or duration of the spring bloom, could alter springtime food inputs to the diverse, largely endemic benthos for which this lake is famous. However, whereas springtime benthic inputs may decrease as ice cover changes, reduced summertime inputs to the benthos seem less likely.

Ultimately, future changes in ice dynamics could also jeopardize reproduction and recruitment of the lake's top predator (box 1), the Baikal seal (*Phoca sibirica*), the only exclusively freshwater seal in the world. Earlier spring ice-off will threaten both adult fertility (box 1) and rearing of the seal pups. Born and reared on the ice in snow-ice caves, pups are concealed and protected from avian and terrestrial predators while the pups molt and mature (Pastukhov 1993). Spring precipitation falling as rain and warmer air temperatures could eliminate the pups' refuge from predators by causing premature disintegration of the snow-ice caves. A decline in seal abundance resulting from this scenario and a decline in adult fertility (box 1) could potentially drive changes in the abundances of organisms at lower trophic levels (e.g., golomyanka, the preferred prey of the seal), but such relationships have yet to be examined.

In summary, of all abiotic drivers, changes in ice dynamics at Lake Baikal will most likely elicit the greatest ecological effects, as has been argued for arctic lakes and marine waters surrounding the Antarctic peninsula (Clarke et al. 2007, Smol and Douglas 2007). But, among the world's lakes, the sensitivity of Baikal's pelagic food web to climate change is unique. This is the only lake where both the dominant primary producers and the top predator are highly dependent on ice for both reproduction and population growth. An important caveat is that this ecological dependence on ice in Lake Baikal is more sensitive to earlier loss of ice in spring than to later formation of ice in winter, although ice cover from 1869

Box 1. Effects of climate change on the pelagic food web and the top and bottom trophic levels of Lake Baikal.

All members of Lake Baikal's pelagic food web (see panel a in the figure; Yoshii et al. 1999) are endemic at the species or subspecies level (but see Genkal and Bondarenko [2006] regarding diatoms), and each will most likely be affected by climate change. The Baikal seal (panel b) and the endemic diatoms (panel c), representing the top and bottom trophic levels, are particularly vulnerable, however, because their reproduction and recruitment requires ice in early spring (figure 4) and ice off will continue to come sooner. In years when ice off occurs exceptionally early, adult seals, which mate and give birth on the ice, are forced off the melting ice into the water before molting is completed. Molting, an energetically expensive process, is prolonged, and this in turn reduces female fertility by as much as 60% (Pastukhov 1993). In addition, warming of the upper water layer during the summer-stratified season could disrupt trophic linkages between organisms in the photic zone and vertical migrators. The golomyanka (*Comephorus*, two species of sculpin fish) that make up 95% of the total pelagic fish biomass, plus the pelagic amphipod *Macrohectopus*, migrate vertically at night, ascending from deep depths (300 to 1600 meters) into the top 50 meters of water to feed on the dominant crustacean grazer, the copepod *Epischura*, which is another vertical migrator. Based on depth-distribution studies of the golomyanka and the pelagic amphipod (Sideleva 2003), which are both cold-water stenotherms, they will probably avoid the warmer upper waters, possibly causing their food intake to decline and the seal to dive deeper for its prey (*Comephorus*). Finally, warmer surface waters could cause a decrease in flesh firmness of the omul (*Coregonus autumnalis migratorius*), a commercially valuable whitefish that feeds on larval *Comephorus* and crustacean zooplankton in upper surface waters. Photographs of the seal and endemic diatoms were provided courtesy of Vadim Kantor, Greenpeace, and Galina Kobanova, respectively. The food-web diagram was modified with permission from Yoshii and colleagues (1999), © 2008 by American Society of Limnology and Oceanography.



through 2000 shortened more in winter (11 days later formation) than in spring (7 days earlier loss) (Shimaraev et al. 2002). Nevertheless, reducing the period of winter ice cover will very likely amplify warming of the water column and increase the exposure of open water to wind activity, eliciting the effects described below.

Water temperature. By 2100, the surface water temperatures of Lake Baikal during summer and fall could be more than 4.5°C warmer than they are today. This prediction is based on the projected increase in air temperature for the Baikal region (table 1), coupled with the observation that mean surface water temperature in summer warmed 1.6°C more than did mean summer air temperature during the last 60 to 100 years (Shimaraev et al. 2002, Hampton et al. 2008). Earlier ice-off (Shimaraev et al. 2002), which allows more heat to accumulate in the upper mixed layer, probably contributed to the rapid warming, as has been described for Lake Superior (Austin and Colman 2007).

Total PPR in Lake Baikal will most likely increase with higher water temperatures and increased stratification, as it has in the past (Shimaraev and Mizandrontsev 2004), and as is predicted for arctic lakes (Wrona et al. 2006). Although Lake Baikal is below the Arctic Circle, the Baikal region shares many characteristics with the terrestrial Arctic, such as extreme variability in weather, permafrost within the watershed, and long seasonal duration of ice. Likewise, similar changes are predicted for climates of the Baikal region and the Arctic. Analyses of 20th-century sediments have revealed a recent increase in PPR in some arctic lakes (Michelutti et al. 2005) and seasonal ranges of PPR in Lake Baikal increased by as much as 25% to 275% from the 1980s to the 1990s (Izmest'eva et al. 2000), with algal biomass (chlorophyll *a*) tripling during the summer between 1979 and 2003 (Hampton et al. 2008). Paleolimnological analyses performed in Lake Baikal show that diatom production during warm periods greatly exceeded production during cold intervals. For example, during one warm interval (i.e., 8.8 thousand years ago) when surface waters were estimated to be about 2°C warmer than they are now, pelagic phytoplankton biomass was eight times higher than at present, according to analyses of sedimentary diatoms uncorrected for differential rates of dissolution (Shimaraev and Mizandrontsev 2004). This greater diatom production may have been stimulated by increased nutrient inputs due to melting permafrost within the watershed (see below).

Importantly, future increases in primary production in Lake Baikal may be accompanied by a 3- to 1000-fold decrease in the size of the dominant primary producers as algal species composition shifts away from diatoms, some of which are unusually large, toward autotrophic picoplankton (APP) and small diatoms (Popovskaya 2000, Fietz et al. 2005). Autotrophic picoplankton thrive in warm (about 8°C to 16°C), stratified waters, whereas most of Baikal's endemic diatoms do not (figure 4; Kozhova and Izmest'eva 1998, Richardson et al. 2000). Furthermore, experimental work on subarctic phytoplankton communities shows that the photosynthetic

rate of APP (size = 0.2 to 2.0 micrometers [μm]) is more strongly stimulated by increases in temperature than is the photosynthetic rate of the larger nanoplankton (2 to 20 μm) and microplankton (20 to 200 μm) (Rae and Vincent 1998). Likewise, laboratory experiments and fieldwork in Lake Baikal show that warm temperatures are a major driver of picocyanobacteria (*Synechocystis limnetica*) growth (Richardson et al. 2000), and APP abundance increases strongly with enhanced, prolonged stratification of the upper water column during summer and fall (Fietz et al. 2005). In a warmer world, this trend would be likely to continue, with APP annually becoming the numerically dominant phytoplankton group. In contrast, the abundance of the cold-water endemic diatoms *A. baicalensis* and *Cyclotella minuta*, which currently bloom in early spring and fall, respectively, is likely to decrease (Mackay et al. 2006) either because of changes in the quality or duration of ice or because of a prolonged period of summer stratification (see "Wind and mixing," below).

This marked shift in algal size distribution from relatively large diatoms to smaller cells could lead to a reduction in the energy available to the top trophic levels of the pelagic food web. When primary producers are as small as APP, macrozooplankton (mainly copepods in Lake Baikal) are unable to feed efficiently, and an additional trophic level (ciliates, flagellates) is necessary for trophic transfer. Less energy would therefore be available for supporting top predators in this less-efficient, longer food chain. Interestingly, a shift toward smaller phytoplankton cells has already occurred in the nearshore waters of the Antarctic Peninsula, caused by rising temperatures and ice melting; the expected decline in the efficiency of krill grazing may lead to a 40% to 65% decrease in carbon transfer to higher trophic levels (Moline et al. 2004).

At higher trophic levels, warmer water temperatures in Lake Baikal have already been linked to a shift in zooplankton community structure, with implications for nutrient cycling. Recently, Hampton and colleagues (2008) documented a dramatic increase in cladoceran abundance in the pelagial waters of Lake Baikal. Such a shift in zooplankton community structure from copepods to an increasing presence of cladocerans could alter nutrient cycling in surface waters, because cladocerans graze a wider variety of algae and sequester more phosphorus than do copepods (Sommer and Sommer 2006).

Effects of warmer water temperatures on fish include a potential disruption of trophic pathways in the pelagic food web (box 1). Although it could be argued that the vast, deep, cold waters of the lake provide a refuge from thermal stress for Lake Baikal's fish, avoidance of the warmer upper waters by endemic cold stenotherms such as the golymyanka (*Comephorus*) could disrupt trophic linkages between the productive photic zone and deeper waters (box 1). However, some fishes, particularly those that spend their entire life cycle in relatively shallow waters (0 to 50 m), may benefit from warmer temperatures. Work in arctic lakes suggests that warmer waters could elicit the positive effects of increased

growth and survivorship for some fish species, assuming their prey production increases (McDonald et al. 1996). Higher temperatures, however, can also negatively affect the quality of meat harvested from cold-water fish (box 1), and the indirect effects of warmer temperatures on fish may include a reduction in nearshore spawning success, as thawing permafrost exacerbates contemporary shoreline erosion (Kozhova and Silow 1998, Anisimov and Reneva 2006).

Wind and mixing. Changes in wind dynamics cannot be projected at present, but they could profoundly affect the physical and biological structure of Lake Baikal. Wind influences the timing of ice formation in winter, ice breakup in spring, heating and stratification during summer, and the spatial distribution of plankton (Todd and Mackay 2003, Kouraev et al. 2007). Furthermore, wind dynamics drive two different large-scale mixing processes, one of which maintains the lake's most unusual chemical feature—its permanently oxygenated deep water—a feature that has contributed to the evolution of gigantism in some of the lake's rich abyssal fauna (Chapelle and Peck 1999).

Deep-water ventilation, the process conveying oxygen to the deep waters of Lake Baikal, occurs during the ice-free season when cold surface waters exhibit unstable density (i.e., heavier surface water perches on lighter water), and strong east winds (southern basin) trigger coastal downwelling. These conditions result in the approximately 300-m thick surface layer plunging into the deep, permanently stratified water below as pressure alters the temperature of maximum density (Weiss et al. 1991, Schmid et al. 2008). Importantly, such cold, oxygen-rich intrusions do not occur throughout the pelagic zone, but instead are confined to locations near shore, and they occur shortly before ice formation (January, southern basin) and after ice out (June, southern basin), when surface waters are always colder than deep water (Shimaraev et al. 1994, Wüest et al. 2005). Intrusions are brief, lasting 1 day to 2 weeks, and approximately 12.5% of the permanent deep-water layer is renewed each year through this deep-water ventilation process (Weiss et al. 1991, Wüest et al. 2005).

In a future climate, changes in wind speed, direction, or timing could carry this lake far from its current state by altering the deep-water ventilation process. For example, an increase in the speed of wind in the appropriate direction for generating a coastal downwelling would enhance deep-water ventilation and the subsequent movement of nutrients from deep to shallow depths. This movement of nutrients could increase PPR substantially, because internal recycling of nutrients from deep to shallow depths is the same order of magnitude as the total of all external inputs (Müller et al. 2005). In contrast, a reduction in wind strength, a shift in wind direction to one inappropriate for initiating a coastal downwelling, or a change in timing could jeopardize deep-water ventilation and the renewal of oxygen to profundal depths. The lake's giant abyssal amphipods with their high oxygen requirements would very likely be among those taxa most

sensitive to depleted oxygen levels if this were to occur (Chapelle and Peck 1999).

Lake Baikal also exhibits fall (November) and spring (May–June) overturn, as do many temperate lakes, but this mixing is restricted to the top 250 to 300 meters—similar to the ocean (Shimaraev et al. 1994). A thermocline occurs between 10 to 20 m for a brief period (approximately 7 weeks) from late July to early September (Yoshioka et al. 2002); however, strong northwest winds often disrupt summer stratification, generating cold-water upwellings along the western coast and causing surface water temperatures to plunge to 4°C from 14° to 16°C within hours (Kozhova and Izmes'teva 1998). With climate change, stronger wind activity during the period of maximum summer stratification (i.e., August) could potentially deepen the epilimnion (warm, upper mixed layer) as predicted for the Laurentian Great Lakes (Lehman 2002). Alternatively, diminished wind strength or frequency, coupled with warmer surface waters in summer and enhanced density gradients, could reduce water movement or turbulence, causing prolonged summer stratification, as reported for other lakes (e.g., Peeters et al. 2007). Although favorable to APP growth, this situation could adversely affect the biomass of dominant pelagic diatoms. It is hypothesized that a delayed fall turnover resulting from prolonged stratification prevents resting stages of the Baikal diatoms from being resuspended in the photic zone during turnover. Resting stages sink beyond the depth of wind-induced mixing during prolonged stratification, diminishing inocula for fall (*C. minuta*) or spring (*A. baicalensis*) blooms in the upper surface layers (Mackay et al. 2006).

Nutrient loading. Nutrient inputs to Lake Baikal from both the watershed and atmosphere are likely to increase with climate change, which, along with higher temperatures, will enhance PPR. Greater amounts of spring runoff resulting from greater winter precipitation, coupled with the thawing of the permafrost, will most likely increase the loading of nutrients, sediments, and organic carbon (dissolved organic carbon [DOC] and particulate organic carbon [POC]) to arctic lakes (Wrona et al. 2006). These predictions can be extended to Lake Baikal, where the Selenga River draining northern Mongolia, a site where permafrost is already melting (Bohannon 2008), delivers more than 50% of the lake's surface water inputs and approximately 70% of all phosphorus inputs (Callender and Granina 1997). In addition, atmospheric inputs of nutrients resulting from ash from forest fires could increase with climate change. Summer forest fires have already increased in frequency and severity near Lake Baikal: seven of the years between 1998 and 2006 were considered extreme fire years in Siberia (Soja et al. 2007). To the west of the lake, in central Siberia, warmer and possibly drier summers resulting from climate change are predicted to exacerbate the frequency and intensity of forest fires (reviewed by Soja et al. 2007). Prevailing winds in central Siberia blow from west to east, potentially transporting ash and soot—both sources of nitrogen and phosphorus—to Lake Baikal. Despite Baikal's

tremendous volume, atmospheric nutrient inputs during summer would enter the relatively small volume of the lake's thin, oligotrophic epilimnion (less than 3% of total volume) and fuel PPR.

Enhanced inputs of allochthonous DOC and POC from Baikal's rivers (Yoshioka et al. 2002) due to climate change could be especially important because of the potential stimulation of the microbial food web and resultant increases in nutrient recycling and carbon processing (Wrona et al. 2006). An increasing number of studies underscore the high abundance of constituents of the microbial food web in Lake Baikal's pelagic zone (e.g., Sekino et al. 2007), suggesting that this food web is a major contributor not only to pelagic PPR (Straskrabova et al. 2005) but also possibly to secondary production. However, trophic links between the microbial food web and higher trophic levels such as the macrozooplankton (e.g., copepods) have not been identified or quantified, preventing estimates of carbon transfer efficiency from the microbial loop to higher-order consumers.

An important caveat to the projected increase in nutrient loading is that vegetation and human land use will also respond to a warmer, wetter climate, but it is unclear how these changes will alter nutrient inputs to the lake 50 to 100 years from now. A subtle shift in the shrub and herb communities in the northern Baikal region has already been attributed to recent climate change (Anenkhonov and Krivobokov 2006). Substantial changes are projected by the end of the 21st century throughout the watershed, as dry forest ("light" taiga) dominated by Scots pine (*Pinus sylvestris*) and larch (*Larix* spp.) gives way to forest-steppe and steppe, and moist "dark" taiga—dominated by fir (*Abies sibirica*) and cedar (*Pinus sibirica*)—expands (reviewed by Soja et al. 2007).

Although it is unknown how terrestrial changes will affect nutrient loading, it is clear that current measurements of nutrients in the lake, and especially in its tributaries, are sparse and infrequent. More accurate nutrient budgets and monitoring data, in addition to tests for potential iron limitation and colimitation by multiple nutrients, are essential for improving understanding of nutrient impacts in this large, heterogeneous lake (Granina 1997, Mackay et al. 2006). Among nutrients, most evidence suggests, nitrogen currently limits phytoplankton growth (e.g., Weiss et al. 1991, Sekino et al. 2007). However, important spatial and temporal interplay of nutrients other than nitrogen (i.e., phosphorus, silica) can control life-cycle processes and population growth of Baikal's diatoms in complex ways (Jewson et al. 2008).

Synergisms between climate change and other anthropogenic stressors

Many additional anthropogenic stressors, including non-point-source pollution, ultraviolet radiation, and invasive species, have the potential to act synergistically with climate change to adversely affect freshwaters throughout the world (Schindler 2001). Industrial pollution and cultural eutrophication are of particular concern for Lake Baikal because climate change will probably elevate chemical inputs.

Furthermore, the lake's distinct features—for example, oligotrophy, cold waters, long residence time, a long pelagic food chain, the high seismicity of the region, and great endemism—heighten its vulnerability to these stressors.

Industrial pollution. Climate change will most likely exacerbate the loading of industrial pollutants such as polychlorinated biphenyls (PCBs) and dioxins into Lake Baikal because soil warming and thawing of the permafrost within the lake's airshed and watershed—already documented in some areas (Bohannon 2008)—could augment the release of stored chemicals. In addition, ground subsidence may endanger industrial infrastructure, amplifying the frequency of spills of pollutants. A recent model calculating the hazard in 2050 from thawing permafrost in Russia predicts that the highest level of hazard will occur at multiple Siberian sites, including the Irkutsk region southwest of the lake (figure 5; Anisimov and Reneva 2006).

The Irkutsk region, containing an industrial corridor with chemical plants and aging industries, lies within the lake's airshed (figure 1), and recent modeling and field sampling suggest that PCBs from within this industrialized corridor (Mamontov et al. 2000, Kuzmin et al. 2005) are carried into the southern basin of the lake on prevailing winds (Mamontov et al. 2000). Although concentrations of PCBs are low in the lake water, body burdens are high in the Baikal seal and in the breast milk of humans in the region who ingest fish up to seven times per week (Kuzmin et al. 2005). Likewise, concentrations of perfluorochemicals (PFCs) in Baikal seals increased in recent years, suggesting ongoing contamination, and chemical analyses indicate a local source of this pollution (Ishibashi et al. 2008). Other potential local sources of pollutants include the Trans-Siberian railroad, now transporting oil along the southern and eastern shores of the lake, and a large deteriorating pulp mill on the southern lake shore (figure 1). Although predictions at small spatial scales (e.g., Trans-Siberian railroad) are not possible using the permafrost hazard model, the modeling effort highlights the potential jeopardy that rail tracks, an aging industrial infrastructure, pipelines, and roads may face when the ground settles unevenly and terrain is distorted by thawing permafrost. These hazards, plus the high seismicity of the region, underscore the likelihood of industrial accidents further contaminating the lake in the future. Unfortunately, the long residence time of the lake (377 to 400 years) and its cold average temperature (5°C surface temperature, southern basin) guarantee that the legacy of such accidents would remain for centuries.

Cultural eutrophication. Climate change is also likely to promote changes in land use and shoreline integrity that could accelerate cultural eutrophication of Lake Baikal. As climate warming continues, ice thickness and coverage in winter will continue to wane, preventing transport of essential supplies across the ice to shoreline villages. This, in turn, will speed the construction of land-based roads to villages to ensure the delivery of goods in winter, and these roads could

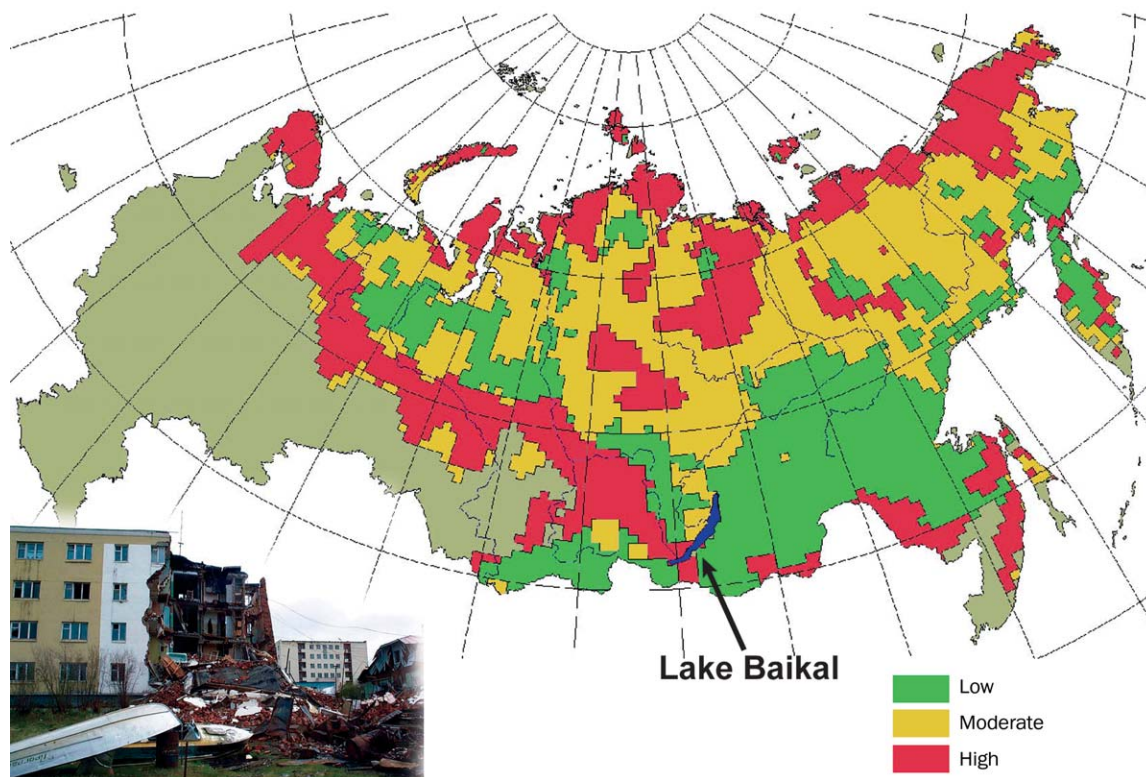


Figure 5. Permafrost hazard map for Russia predicting hazard (low, moderate, high) to human infrastructure (roads, pipelines, factories, buildings) from thawing permafrost using predictions from the Geophysical Fluid Dynamics Laboratory climate scenario for 2050 (Anisimov and Reneva 2006). Note that the high hazard region surrounding the southern basin of Lake Baikal includes the industrial corridor of the Angara River. The photograph shows a building in northern Siberia that was damaged by permafrost thawing and ground slumping (Anisimov and Reneva 2006). The map and photograph were published originally in *Ambio*; they are provided courtesy of Oleg Anisimov and Vladimir E. Romanovsky, respectively.

promote localized development and near-shore eutrophication. Still another example of land-use change with climate warming is greater tourism and more building construction, which is already occurring in localized areas on highly erodible soils. Finally, thawing permafrost resulting from climate change (figure 5) will exacerbate nearshore inputs of sediments and nutrients that have been elevated in recent decades by anthropogenic shoreline erosion. This coastal erosion—yielding sediment inputs estimated at 400,000 tons in 1984—began in 1956 after the construction of a hydroelectric dam on the Angara River elevated the lake’s water level by 1 m (Kozhova and Silov 1998).

The potential for climate change to enhance cultural eutrophication of Lake Baikal is particularly important because the lake’s current trophic status may be changing. Although offshore waters of Lake Baikal are still oligotrophic (Tarasova et al. 2006), the trophic status of the entire lake is unclear because reliable measurements of nutrient concentrations are rare and intermittent (Granina 1997). Phytoplankton biomass has increased over time in shallow bays and in the Selenga River delta (Popovskaya 2000), as well as in the southern basin approximately 3 kilometers offshore (Hampton et al. 2008), and these trends could be interpreted as evidence of

near-shore eutrophication. However, a recent detailed study of phytoplankton biomass and community structure across the three basins concluded that enhanced stratification during summer was responsible for elevated algal biomass in nearshore waters (Fietz et al. 2005). Whatever the driver, increased algal biomass in shallow waters could endanger benthic biodiversity by shifting the energy source of the benthos and by altering benthic community structure and biomass (Chandra et al. 2005).

Research needs

Although much essential research is needed at Lake Baikal, strengthening and expanding long-term monitoring efforts should be a top research priority. Rapid, ongoing climate change will drive systematic changes in a variety of Lake Baikal’s critical characteristics (e.g., ice cover, thermocline depth, deepwater mixing, in-lake nutrient concentrations and inputs), but the pace and consequences of those changes are uncertain. Long-term changes in lake structure and function may be in progress (Hampton et al. 2008) and could carry the lake far from its current state. Implementation of cost-effective mitigation measures will very likely depend on early detection of emerging trends.

Multiple research teams are conducting long-term monitoring of primarily physical and biological factors and processes. The Institute of Biology at Irkutsk State University monitors water temperature in the upper mixed layer, Secchi transparency, plankton abundance and species composition, and chlorophyll *a* (Izmest'eva et al. 2006, Hampton et al. 2008); the Swiss Federal Institute of Aquatic Science and Technology, the Institute of Applied Physics at Irkutsk State University, and the Russian Academy of Sciences Limnology Institute in Irkutsk determine temperature-depth profiles and current velocity for detecting deepwater renewal (e.g., Shimaraev et al. 1994, Schmid et al. 2008); and the Russian Academy of Sciences Limnology Institute in Irkutsk quantifies nutrients, plankton, benthic invertebrates, and fish. Importantly, however, most sampling by these teams is concentrated in the southern basin, because time, money, and physical effort (especially in winter) constrains work in the more remote central and northern basins.

We suggest that ongoing monitoring efforts expand to include key variables that control ecosystem function but are not measured now (or are measured only intermittently). These variables include nutrient concentrations and external loading rates from the atmosphere and surface waters, particularly the Selenga River. In addition, annual surveys of the lake's top pelagic predator, the Baikal seal, which ended in the early 1990s, should be renewed because of this animal's sensitivity to changes in ice cover and the potential effects on food-web structure. Also, less-frequent but periodic sampling of bioaccumulative contaminants (PCBs, PFCs) in seals will reveal the extent to which climate change enhances the release of these compounds into the lake ecosystem. Quantifying key meteorological drivers, including wind speed and insolation at the lake surface rather than at nearshore sites would benefit physical-biological modeling efforts. Finally, it is essential to detect the effects of warmer water temperatures on Baikal's biota, including potential invasibility by non-native, warmwater species that currently occur primarily at warm river mouths. Lake Baikal is a notable outlier in temperature-biodiversity relationships (Allen et al. 2002)—it exhibits the highest biodiversity of any lake but at an extremely cold average temperature. The study of this assemblage of cold stenotherms, including the littoral-sublittoral benthos where three-quarters of the lake's species reside, should accelerate to beat the pace of rapid warming that changes such communities. Comparing long-term changes in abundance and phenology of selected species in the southern basin with their counterparts in the northern basin where temperatures are colder and ice coverage has a longer duration may provide a natural setting for testing biotic effects of climate change.

Ongoing monitoring will be additionally strengthened by securing long-term funding for sustaining existing work, coordinating efforts among research teams, and employing new technologies. Genuine cooperation and joint financial support between the international scientific community and Russian scientists working on the lake are urgently needed to maintain current monitoring efforts. Such cooperation was

achieved successfully during the 1990s through the Baikal International Center for Ecological Research, a consortium of scientists from Russia, the United Kingdom, Switzerland, Belgium, Germany, Japan, and the United States (e.g., Mackay et al. 2005, Jewson et al. 2008, Schmid et al. 2008). Also, a comprehensive monitoring plan that unites and expands existing endeavors will enhance efficiency and efficacy. Finally, careful adoption or continued use of new technology such as satellite imagery for detecting long-term changes in ice dynamics (Kouraev et al. 2007) and *in situ* instruments with real-time, continuous sensors for quantifying key limnological variables (e.g., water temperature, chlorophyll *a*, pH, conductivity) could ultimately save money and enhance understanding of ecosystem processes across multiple time scales.

The choices of Russians, many of whom have shown exceptional dedication to the lake in the past and are actively concerned about its welfare today, will determine future local impacts on the Sacred Sea. However, limiting climate change, which is arguably the most pervasive threat to the lake, can be achieved only through international commitments and concerted action, including the involvement of the world scientific community.

Acknowledgments

The Lake Baikal Working Group, supported by the National Center for Ecological Analysis and Synthesis (NCEAS), a center funded by the National Science Foundation (DEB-0072909), the University of California, Santa Barbara, and the State of California, produced this article. Harriet Alexander, Cheryl Hojnowski, Ashley Ortiz, Julia Shalnova, Adrien Smith, and Kelima Yakupova provided valuable technical assistance and were funded by Wellesley College and NCEAS. We thank Alexei Kouraev, Mikhail Shimaraev, and Jennie Sutton for references to the Russian literature; Bernie Gardner and Martin Schmid for insights into deep-water ventilation; and Suzanne Fietz, David Jewson, Nick Rodenhouse, Maxim Timofeyev, and three anonymous reviewers for greatly improving an earlier version of the manuscript.

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Marianne V. Moore (e-mail: mmoore@wellesley.edu) is with the Department of Biological Sciences at Wellesley College in Massachusetts. Stephanie E. Hampton is with the National Center for Ecological Analysis and Synthesis at the University of California in Santa Barbara. Lyubov R. Izmes't'eva, Eugene A. Silov, Ekaterina V. Peshkova, and Boris K. Pavlov are with the Scientific Research Institute of Biology at Irkutsk State University, Irkutsk, Russian Federation.