8 THE BLUE EYE OF SIBERIA

От Байкала начинается сибирская поэзия.

Siberian poetry begins from Lake Baikal.
—Anton Chekhov, in letter to A. N. Pleshcheyev, 1890

Baikal, or the Sacred Sea as it is known in Russia, is the largest, deepest, and most ancient of freshwater ancient lakes. At Baikal's beginning, usually considered to have been about 25 million years ago, our planet was a quite different place—the fauna, climate, and even continents were not as they are today.

If, for example, you were somehow to find yourself by the North American seaside of that time, you might encounter *Pelagornis sandersi*, a seabird with a wingspan of over twenty feet, about the same as an Andean condor and a wandering albatross placed wing tip to wing tip and measured together. Venture inland a little ways and wildlife would likely have been common, as human hunters would be far in the future, but the mammalian grazers would have seemed odd. Camels, or at least members of the camel family, were abundant. South America, where the Camelidae had not yet arrived and given rise to llamas, had an even more exotic fauna in the late Oligocene and early Miocene (the Oligocene-Miocene boundary was 23 million years back, just after Baikal appeared), but would have been hard to get to. The Isthmus of Panama was still beneath the waves, and the seas were far from welcoming. *Megalodon*, the fifteen meters or so relative of today's great white sharks, was widespread.

Still, South America might well have been worth the trip. Among the stranger sights would have been a collection of gigantic, plant-eating, armadillo-like creatures—the glyptodonts. Your greatest worry might have been a bird, two or three meters tall and flightless—a sort of ostrich meets *Tyrannosaurus rex*. Known colloquially as terror birds, various species of these dinosaur-esque hunters preyed and scavenged across much of South America all the way through Baikal's early years.

Primates were well established in both South America and the old world 25 million years ago, but our own family, the Homininae, would not appear on the drying savannas of Africa for another 15 million years or more. Even the apes (the Hominoidea) had only just appeared, splitting off from the other old-world monkeys and their kin.

The weather was balmy in the late Oligocene, and some of the higher latitude regions had much more pleasant winters than they have today. In general, the climate varied less between the poles and equator. Ice had by this point covered Antarctica in a permanent blanket, but the glaciers later to dominate the far north would not become established for many millions of years. While the continents were close to their current positions, they were not quite there. The Americas, for example, were a little closer to Europe and Africa than they are today;

the Atlantic was still opening up, a result of slow but steady spreading along the mid-Atlantic Ridge.

Baikal too was very different 25 million years ago. In fact, while the age of Baikal is typically given as 25–30 million years, the rift in which it is located first appeared and filled with water much earlier, about 70 million years back. Thus, an early form of Baikal, archeo-Baikal (figure 8.1), may have had dinosaurs along its banks, perhaps the eight-meters-long duck-billed dinosaur *Amurosaurus*, for example (figure 8.2). Archeo-Baikal possessed a moist, subtropical climate, and while probably ecologically significant in its time, we would not recognize it as the modern lake. It was a string of smaller bodies of water, at most tens of meters deep, not consistently connected and occupying only the southern basin of today's lake. Still, there is some evidence that a few of the invertebrate lineages found in Baikal today got their start in the time of archeo-Baikal.

It is the Baikal that took shape 25–30 million years ago that is widely treated as recognizably today's lake, despite differences from the Baikal we know, so that is the time frame I have emphasized when discussing the lake's beginnings. Sometimes known as proto-Baikal (figure 8.1), it was initially two separate lakes, one in the modern south and central basins, more or less, and one in the farther reaches of the north basin, with the intervening areas largely dry. Owing to uplifting of surrounding land, however, the lake had become deeper, reaching depths of hundreds of meters in both sections.

During the proto-Baikal period, the climate remained much warmer than ours, but it was nonetheless drying and cooling. Along the shores of the lake, forests were gradually replaced by steppe and desert-steppe landscapes. The lake itself

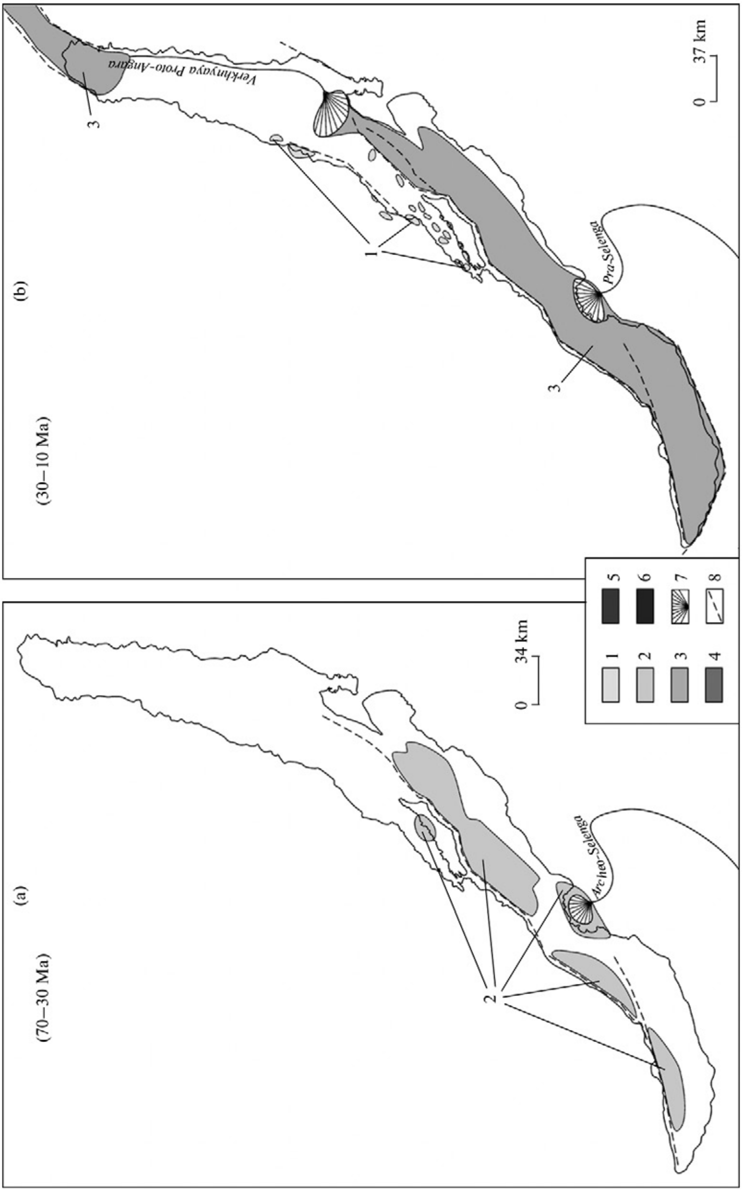

(a)
(70–30 Ma)
Archeo-Selenga
0 34 km
(b)
(30–10 Ma)
Pra-Selenga
Verkhnyaya Proto-Angara
0 37 km
1
2
3
4
5
6
7
8

Figure 8.1

The early days of Lake Baikal (the outline of the modern lake is shown, but only the shaded areas had water): (a) archeo-Baikal stage, close to 70 million years ago; (b) proto-Baikal stage, about 25 million years ago. Depths and substrates: (1) a few meters deep, (2) up to tens of meters, (3) up to a few hundred meters, (4) up to several hundred meters, (5) up to 1,000 meters, (6) > greater than 1,000 meters, (7) deltas, and (8) main faults. *Source:* Reprinted with minor modifications with permission from Springer Nature, from Mats et al., "Late Cretaceous-Cenozoic History of the Lake Baikal Depression and Formation of Its Unique Biodiversity," *Stratigraphy and Geological Correlation* (2011).

was not static during the long period of proto-Baikal and continued to evolve. Approximately 10 million years ago it became a single, continuous body of water with the submergence of the entire northern basin. Other parts of the lake continued to deepen, reaching over 500 meters.

Dramatic changes occurred in the climate and lake starting about 3.5 million years ago, which also marks the end of the

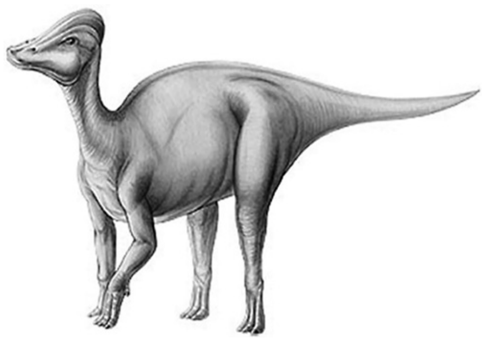


Figure 8.2

Amurosaurus riabinini, a duck-billed dinosaur found in eastern Russia at the time of archeo-Baikal. *Source:* Institut Royal des Sciences Naturelles de Belgique.

proto-Baikal period. With continued cooling and the onset of cycles of "ice ages" about 2.6 million years ago, Siberia moved toward its modern climate, or an even colder one during episodes of glaciation. Baikal, though, was never glaciated, even when regularly covered by ice during both glacial and interglacial episodes, including the interglacial we are in today. It did become much less productive when the glaciers grew, with diatom abundance in sediments greatly reduced as ice a mile deep spread across the northern reaches of the planet. It also continued to deepen as the Pleistocene proceeded, reaching about1,000 meters in the south basin approximately 1.6 million years ago, at the latest. But its depth went up and down with the advances and retreats of the Pleistocene's massive blankets of ice too. The ice affected precipitation, winds, and the flow of rivers around Baikal and across most of the planet.

It was surprisingly recently, in only the last 150,000 years, that Baikal became the ultradeep, consistently oxygenated lake that we know today, now 1,642 meters at its deepest point. There are a few other cool, deep lakes in the northern reaches of our planet, some fairly old (see figure P.1), but only Baikal has evolved a distinctive deepwater fauna and an open water ecosystem dominated by a unique set of organisms.

OFFSHORE BAIKAL

Some of the key ecological players in Baikal's extensive offshore waters are utterly unlike those of any other water body. And they seem to get odder as you work your way up the food chain.

The base of the food chain, at least in terms of animals, is a species endemic to Baikal but not especially peculiar: the

1.5-millimeter copepod crustacean *Epischurella baikalensis* (known until recently as *Epischura*). Copepods are tiny crustaceans (the same group as crabs, shrimp, and crayfish) that are usually abundant in large lakes and seas, though most lakes lack an endemic species. When I think of these creatures, I always think of North Atlantic right whales because a former lab mate of mine spent many hours poring through copepod samples in order to better understand the ecology of right whales, which were feeding on the copepods. I still find it perplexing that despite their diminutive dimensions, these tiny crustaceans can be abundant enough to support warm-blooded animals as massive as whales. In Baikal, there are of course no whales (there is a seal, which we will come to), but *Epischurella* is indeed ecologically dominant among zooplankton, the lake's tiny open water animals, and enormously important as food for larger creatures. It is not common in sheltered bays, especially during the summer, but in the open waters of the lake, *Epischurella* often comprises more than 90 percent of the zooplankton. It feeds on a mixture of open water algae and microorganisms such as ciliates (with ciliates possibly more important than long assumed), and is popularly credited with keeping the water clean and clear.

The great majority of the *Epischurella* are found, year-round, in the upper 250 meters of the water column—a range extending deeper than the bottom of most lakes, but of course encompassing only the shallower portions of Baikal. In the summer, *Epischurella* exhibit "diel vertical migration," coming within about 5 meters of the water surface at night and heading deeper during the day. This is a widespread phenomenon that is observed in the zooplankton of many water bodies. It is generally thought of as an adaptation to avoid visually hunting predators during the day, when the waters just below the surface are well lit, while allowing feeding on shallow-dwelling algae at night. *Epischurella* is well adapted to Baikal's chilly waters and will tolerate only a narrow range of temperatures, doing poorly above about 15°C.

There are exceptional long-term data sets for *Epischurella* as well as other planktonic species and the waters they inhabit owing to a remarkable long-term sampling effort. Three generations of Siberian biologists, all members of a single family, began collecting physical and biological data in Baikal in 1945 and continued into the twenty-first century (figure 8.4). At least once a month, and usually every seven to ten days, they collected nine sets of samples at preestablished depth intervals from 0–250 meters at a site about 2.7 kilometers offshore, where the water is 800 meters deep. Their collection site is a little way off the head of the Angara River, which is shown in figure 8.3, upstream from Irkutsk. This would be an impressively consistent record in an easily accessed subtropical location—but in a sometimes frigid and difficult locale like Baikal it is heroic. Winter sampling required walking over the ice at temperatures that would be daunting for even my hardiest Canadian relatives. Occasionally the ice was not thick enough to walk on yet was impassable by boat as well, resulting in virtually the only situations in which sampling did not take place. Fortunately, such conditions were infrequent and temporary.

Data collection persisted not just through difficult weather but also through the reign of Soviet leader Joseph Stalin, the end of the Soviet Union, and a collection of other national and international upheavals and transitions. The initiator of

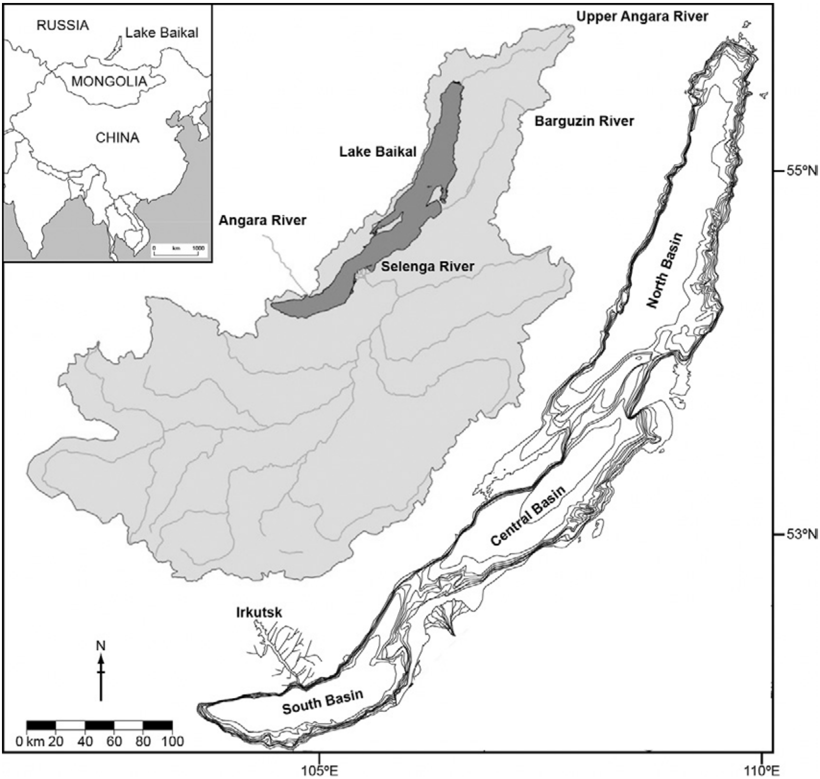


Figure 8.3

Modern Lake Baikal and its major drainages, with depth contours. *Source:* Reprinted with minor modifications from Swann et al., "Changing Nutrient Cycling in Lake Baikal, the World's Oldest Lake," *Proceedings of the National Academy of Sciences* (2020). Published under a Creative Commons CC BY 4.0 license (https://creativecommons.org/licenses/by/4.0).

Figure 8.4
Left to right: Lyubov Izmest'eva, as a child, with her grandfather, Mikhail Kozhov, 1955; Olga Kozhova, about 1975. *Source:* Lyubov Izmest'eva.

the effort was Mikhail Kozhov, a professor at Irkutsk State University and author of a famous book about Baikal from the early 1960s. His daughter Olga Kozhova continued the program and took a position at Irkutsk State too, followed by her daughter, Lyubov Izmest'eva, who has now retired from that institution (though data collection continues at a slightly reduced frequency). The family's long-term data have enabled a variety of analyses, including quantitative assessments of how zooplankton communities have changed with a warming climate and shrinking ice cover. Some of this work suggests a decline in *Epischurella* relative to other zooplankton species as the lake has warmed, which we will return to.

The next link in the food chain is also a crustacean and member of the zooplankton, but larger and more unusual. This is the gammarid amphipod, *Macrohectopus branickii*, a creature up to about thirty-eight millimeters long and a peculiar outlier in one of Baikal's most extraordinary radiations. Among the more than 265 species of gammarids in Baikal (the number is tough to pin down), smaller radiations in Titicaca and a few other lakes, and another radiation among the caves and underground waters of Europe, this is the only freshwater gammarid amphipod to have taken up an entirely open water existence and become a key component of an offshore food chain.

The evolution of *Macrohectopus* and the other Baikal gammarids was touched on in the first chapter, but the entire group merits a little more attention. If nothing else, the gammarids are noteworthy for being a truly ancient-ancient lake radiation. Exactly how long Baikal's gammarids have been in the lake is not known with accuracy, as the dating of their radiations is a work in progress, but they may be as old as the modern lake itself and could have been in archeo-Baikal.

The idea that Baikal's gammarid radiations were the result of repeated colonizations by non-Baikalian lineages has long been accepted, but there has been little agreement about just how many times this happened. A trend has emerged, however, for estimates to settle at two colonization events. This includes the report of the most comprehensive study yet, based on extensive sequence data, by a large international group including Sergey Naumenko at Moscow State University and Lev Yampolsky at East Tennessee State University as well as a follow-up study also involving Yampolsky. Their work emphasizes the radiation that resulted from the second invasion, the Acanthogammaridae and allies. This contains much of the ecological diversity seen in Baikal's gammarids, such as the "abyssal" species found in the depths of the lake and species

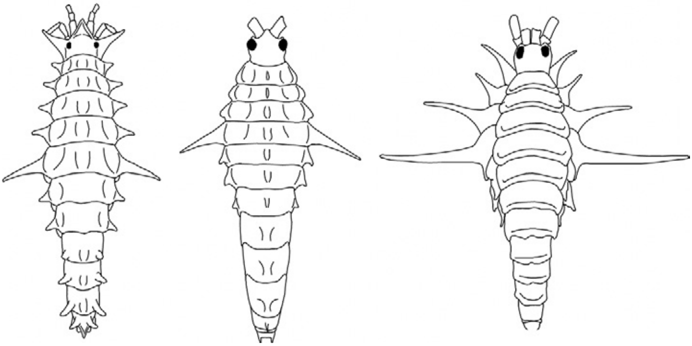


Figure 8.5

Left to right: Convergent body armature in gammarids from the Caspian Sea (*Axelboeckia spinosa*), Lake Baikal (*Acanthogammarus lappaceus*), and Lake Titicaca (*Hyalella armata*). *Source:* Reprinted with minor modifications with permission from Springer Nature, from Copilaș-Ciocianu and Sidorov, "Taxonomic, Ecological and Morphological Diversity of Ponto-Caspian Gammaridean Amphipods: A Review," *Organisms Diversity and Evolution* (2022).

that live parasitically inside the brood chambers of a different amphipod (brood chambers are a little bit like the pouches of kangaroos). It also includes those gammarids most associated with Baikal: heavily armored species like *Acanthogammarus victorii*, which are convergent with species in Titicaca and the Caspian Sea (figure 8.5).

One finding emerging from studies of this main Baikalian gammarid radiation is that speciation and diversification rates were highest close to its start. This is satisfying in its consistency with theory, which predicts most rapid diversification when the ecological opportunity is greatest—sometimes known as an "early burst." But it makes settling on the relationships among the major lineages, which diverged then, especially difficult. It also creates challenges for working out the relationships with non-Baikalian gammarids. Things happened fast at the start followed by millions of years of further evolution that tend to throw a genetic smoke screen in front of the earliest events. It is as if evolution were playing the children's game of telephone, where one child whispers a phrase to another one, who then whispers it to another child, and so on. After passing between a dozen or so players, the phrase may be changed yet easily recognizable or almost entirely different. The more players in telephone, or the more generations since the burst of an adaptive radiation, the greater the potential for change and the more difficult it is to make out the phrase, or relationships, at the start.

The older but less extensive radiation, known as the Micruropodidae, contains mainly species that are "fossorial," living buried in the sediments most of the time and possessing smooth bodies well suited to such a lifestyle. Unexpectedly, it is in this group that repeated analyses have placed the open water–living *Macrohectopus*. It is a genuinely puzzling result that a species with a wildly distinctive form and ecology should be found to have evolved from a group in which shape, body features, and ecology are relatively homogeneous and based on a life within the sediments—rather than from a larger set of species exhibiting much greater diversity. There is no clear explanation for this odd state of affairs as yet, but one observation may prove telling. One of the burrowing species, *Micruropus wahli*, has been caught in large quantities in surface waters at night. Perhaps habits of this sort in members of the Micruropodidae facilitated the evolution of a free-swimming open water feeder. It is likely also pertinent that in this older lineage, there was abundant time for *Macrohectopus* to diverge and adapt to its new lifestyle.

In addition, over such a long expanse of time, related species that might have clarified the evolution of *Macrohectopus* may have gone extinct in one of the many ecological upheavals that punctuate Baikal's long history. Analyses of sequence data indicate strong natural selection has taken place on the genes of *Macrohectopus*, possibly in support of adaptations to an active planktonic mode of life as well as the low temperatures and high-pressure characteristic of the deep open waters in which it often occurs.

Macrohectopus is so abundant in the modern Baikal that it is frequently compared to krill, the crustacean of the Southern Ocean that is the key food source for a long list of marine mammal and bird species as well as the focus of a human fishery. Abundant and large enough to have substantial energetic value, *Macrohectopus* is a critical food for several Baikal fishes, including the omul, the whitefish that has been the basis for Baikal's most important fishery (and I understand why; omul really is delicious).

Like the smaller plankton on which it feeds, *Macrohectopus* performs vertical migrations. Occupying a wide range of depths from the surface to 700 meters, it typically moves from deeper waters during the day to the upper 50 meters of the water column at night. The density of its aggregations is noteworthy, as is the synchronization of its vertical migrations, which can involve ascents as rapid as 4 meters per minute. Keeping in mind this pace corresponds to one to two hundred body lengths, it is about the same as a human swimmer of 1.5 meters height rising at 150–300 meters per minute. Anyone who has tried to free dive to any depth or even just do some speedy lengths in a pool can appreciate just how fast that is.

Not every *Macrohectopus* makes exactly the same migration, though. It is the large females that move the farthest. Males, which are only a fraction of the size of females, tend to make a shorter vertical migration. The movements of the juveniles, who typically do not go as deep during the day, are also less extreme than those of the adult females.

One of the most abundant fish in Baikal feeds extensively on *Macrohectopus* and is equally exceptional, as it is also an open water species from a group that almost always sticks to the bottom. It is also simply a strange creature, the golomyanka, *Comephorus baicalensis*. It is the most unusual member of a radiation of sculpins, an ancestrally marine group of fishes that have evolved into 100 or so freshwater species across the Northern Hemisphere, but that are nowhere as diverse in ecology or form as in Baikal.

Most freshwater sculpins, members of the superfamily Cottoidea, live along the bottom of streams, rivers, and lakes in relatively shallow waters. In Baikal, they have diversified into about thirty-three species found nowhere else, evolving in two novel ecological directions: into the depths, the abyss of the lake, and the open water zone. Given how thoroughly they dominate the fish community of each zone and how few competing species are present, the ecological excursions of this lineage of Siberian sculpins are likely another example of opportunity-driven adaptive radiation. The sculpins comprise well over half of the fifty-two species and subspecies of fish that are native to the lake.

Compared to the great age of the gammarid diversification, the radiation of the sculpins is relatively recent. Estimates of the radiation's timing are still being refined, but it seems clear that it took place in the essentially modern version of Baikal, most likely between roughly one and five million years ago, but a few million years earlier is quite possible. In another departure from the patterns seen in the gammarids, Baikal's sculpins appear to have all evolved from a single ancestor. Thus, they are all more related to each other than to any non-Baikal sculpin. Most likely they evolved from another species of freshwater sculpin from within, more or less, the genus *Cottus*. This placement suggests that the various Baikalian sculpins, currently assigned to different families, will need to have their classification revisited. One point of overlap between Baikal's sculpins and gammarids, though, is the tempo of their diversification. The sculpins diversified rapidly at the start too. Moreover, these groups are linked ecologically in that different species of gammarids are the main prey items for the various species of sculpins; their radiations are connected.

One of the reasons an open water sculpin is considered such an exotic creature is that among fishes, sculpins are notably ill-suited for this way of life. An open water sculpin is almost as biologically incongruous as a celery-feeding shark. The main shortcoming of sculpins when it comes to open water life is that they lack a swim bladder, the organ that most fishes living off the bottom use to maintain buoyancy. Through fine adjustments, many fishes dial up or down the gas present in this organ in order to stay neutral and level, neither sinking nor rising, much as a scuba diver does with a buoyancy compensator. Too little gas in the diver's inflatable vest and the diver sinks; too much and they rocket to the surface, which can be even more dangerous. Sculpins cannot make any such adjustments so they have had to find other ways to keep a stable position in the water column without expending undue amounts of scarce energy. They especially need to avoid sinking, the natural tendency of fish adapted to living on the bottom (still, partially open water sculpins less extreme than Baikal's occur in at least two North American lakes, though seldom mentioned in the literature).

There are a few species of open water sculpins in Baikal, but it is the golomyanka (the big one; there is a second smaller species that we will come to shortly) that shows the most extreme adaptations for maintaining neutral buoyancy. Whereas bottom-dwelling sculpins can have bodies containing less than 3 percent body fat, the adult golomyanka is commonly over 40 percent fat by volume. This is a remarkable amount; a fatty hamburger, for example, is about 20 percent fat, or 30 percent at the most. Cheddar cheese, one of the fattiest of cheeses, is about 33 percent lipid. Brie, which seems to me awfully rich, is about 28 percent. They are all much lighter fare than golomyanka. The golomyanka also has bones that are less mineralized than those of bottom-dwelling sculpins. Reduced bone mineralization and thus density is likely even more important for buoyancy in the other open water sculpin species, none of which have lipid levels at all close to those of the golomyanka. In addition to its high fat levels and reduced bone density, the golomyanka is similar to some deepwater marine fish in having almost no pigmentation. Therefore under some conditions, the tail end of a golomyanka can be eerily translucent.

In most sculpins, females lay their eggs underneath stones; males spray their sperm over the eggs in order to fertilize them and then defend them as they develop. The larvae may be bottom or open water dwelling, depending on the species, but they eventually develop into bottom-dwelling adults. But the golomyanka and the closely related *Comephorus dybowskii*, the little golomyanka, have also modified their reproduction for a fully open water existence. Instead of the male releasing sperm over the eggs after they leave the female's body, the two species have evolved internal fertilization and live birth, completely emancipating both of them from any link to the bottom of the lake.

Both species also show a predictable dietary progression as they develop. At small sizes, they mainly eat the copepod, *Epischurella*, and then shift to the open water gammarid *Macrohectopus* as they grow. This remains the overwhelmingly dominant prey item for little golomyankas, but as they grow larger both species eat golomyanka larvae as well as the larvae of other pelagic sculpins. For the little golomyanka, fish larvae seem to be an infrequent food, but for the larger species they are sometimes the main prey item. Both species participate in the daily vertical migrations of Baikal's open water fauna, following their copepod and gammarid prey as they move toward the surface at night and the depths during the day. The golomyanka go deeper than some, however—sometimes reaching the abyssal depths of the lake. While doing research on coral reef fish, I have sometimes hung in the water of a passage leading from the open ocean to the lagoon of an atoll as schools of open water fishes move onto or off the reef. It is an awesome sight, watching all of that life move past. I imagine that if one could hang in Baikal's water column, it would be an equally beautiful and much eerier procession as the translucent golomyanka make their way up or down, along with dense layers of *Epischurella* and *Macrohectopus*, at twilight and dawn.

Unfortunately for those living alongside Baikal, the golomyanka are solitary creatures and thus difficult to fish profitably. They are of great value, though, to the next step up the food chain to another odd creature to find in a freshwater lake.

Baikal's most famous denizen is the nerpa, *Pusa sibirica*, the only species of seal confined entirely to fresh water. There are seals that occur in freshwater lakes in other places—such as eastern Canada and northern Europe—but they are clearly populations of familiar marine species that occasionally colonize short-lived postglacial lakes. There is one other lake, the Caspian Sea, that is home to a species of seal, but a seal in a vast salty lake usually labelled a "sea" seems less noteworthy than Baikal's nerpa. Anyway, the Caspian seal, *Pusa caspica*, is closely related to the nerpa.

So how did a seal come to inhabit a lake over a1,000 kilometers from the nearest ocean and even more distant if one follows the rivers? The most likely scenario is that the seals swam there from the frigid seas along the north coast of Siberia via the Yenisei River and then Angara River, into which Baikal drains. The DNA sequence data, and shared parasites too, suggest that Baikal seals evolved from adventurous ringed seals that managed to make this ambitious trip. The Caspian seal likely had a similar origin, though separate and independent from the nerpa's. Sequence analyses suggest the nerpa lineage broke off from the ringed seal well after the radiations of the gammarids and sculpins, about 1.15 million years ago, give or take 500,000 years. Thus, the nerpa arrived in Baikal decidedly after the start of the Pleistocene and its cycles of glacial advance and retreat. River flows varied greatly with changes in the glaciers, and huge temporary lakes sometimes came and went. It is possible that these dynamics played a role in the colonization of Baikal by ringed seals, and the Caspian too, although no well-supported scenario has yet emerged.

Owing to Baikal's size and climate, nerpa have been able to establish a life cycle and ecology surprisingly similar to that of other ice-loving seals. These relatively small seals, which reach about 1.65 meters and 130 kilograms, live mainly in the northern and central basins of Baikal, most of the year staying in open water well away from the coasts. Adult animals winter alone on the ice using the thick claws on their front flippers to maintain a hole through which to access air when they are in the water. In February or March, females bear young in a lair made among the snowdrifts and nurse them for 1.5 to 2 months—longer than ringed seals. The life span of the nerpa is also relatively long, sometimes over 50 years. These extended suckling times and life spans are likely a reflection, at least in part, of a great advantage to a seal of life in Baikal: a paucity of predators. Ringed seals, the closest relative of the nerpa, are a key food item for several large predators of far northern seas, including the polar bear and killer whale; Greenland sharks also eat ringed seals. In departing the Arctic Ocean, the nerpa left these voracious and effective predators behind. There are brown bears at Baikal, and they may take an occasional hauled-out seal, but their hunting is nothing like that of the polar bear, an essentially marine animal that achieves much of its annual caloric intake while hunting from the sea ice. Humans hunt nerpa and have likely done so for a long time, but the population seems so far to tolerate the numbers taken, some of which are hunted legally and others illegally.

The resilience of the nerpa to all manner of human insult may well be the seal's most remarkable characteristic—resilience not just to hunting but also to the effects of viruses that we and our animals may have helped spread, and pollutants such as dioxin and mercury. Amazingly for a large mammal in such a constrained environment, the nerpa is an International Union for Conservation of Nature "species of least concern." Some of the population's hardiness may be a result of a stable food source, as nerpa eat a great deal of golomyanka, both the big and small ones. Because there is no fishery for these solitary open water sculpins, their abundance has not been depressed by human removals, which is a serious problem for other marine mammals that compete with human fisheries. But the seals also eat the even more abundant *Macrohectopus* amphipods, and a detailed study of the seal's feeding behavior, published in 2020, has revealed that nerpa are better adapted to this food source than was long appreciated.

Yuuki Y. Watanabe of Japan's National Institute of Polar Research, Eugene Baranov of the Baikal Seal Aquarium in Irkutsk, and Nobuyuki Miyazaki of the University of Tokyo temporarily attached biologging packages to several foraging nerpa in 2018. Each package contained equipment that recorded aspects of the seal's environment and swimming, including a video recorder. Marine mammals that eat open water invertebrate prey typically do so by catching many at a time using adaptations like the baleen of right whales, which sieve copepod prey by the thousands. The data from the foraging seals, however, revealed that they caught *Macrohectopus* one by one—but *fast*, at the highest rates yet recorded for single-prey-feeding aquatic mammals. Seals caught an average

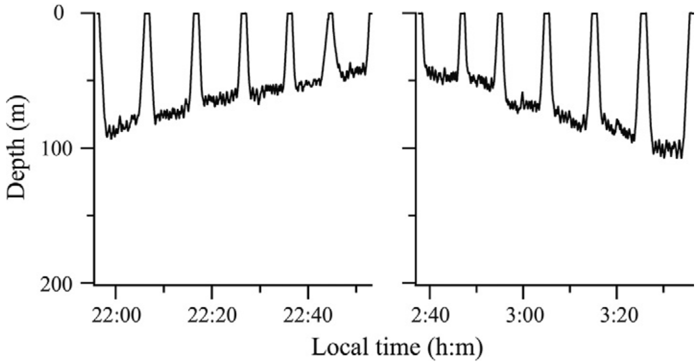


Figure 8.6

Depth data for the foraging dives of individual nerpa in June 2018. As the *Macrohectopus* ascend at dusk, the seals' move shallower, and their foraging depth decreases even within a single dive. The reverse happens as the *Macrohectopus* descend, with dawn's approach (note dusk comes late and dawn early at Baikal's latitude in the summer). *Source:* Reprinted with minor modifications with permission of the National Academy of Sciences of the USA, © 2020, National Academy of Sciences, from Watanabe et al., "Ultrahigh Foraging Rates of Baikal Seals Make Tiny Endemic Amphipods Profitable in Lake Baikal," *Proceedings of the National Academy of Sciences* (2020).

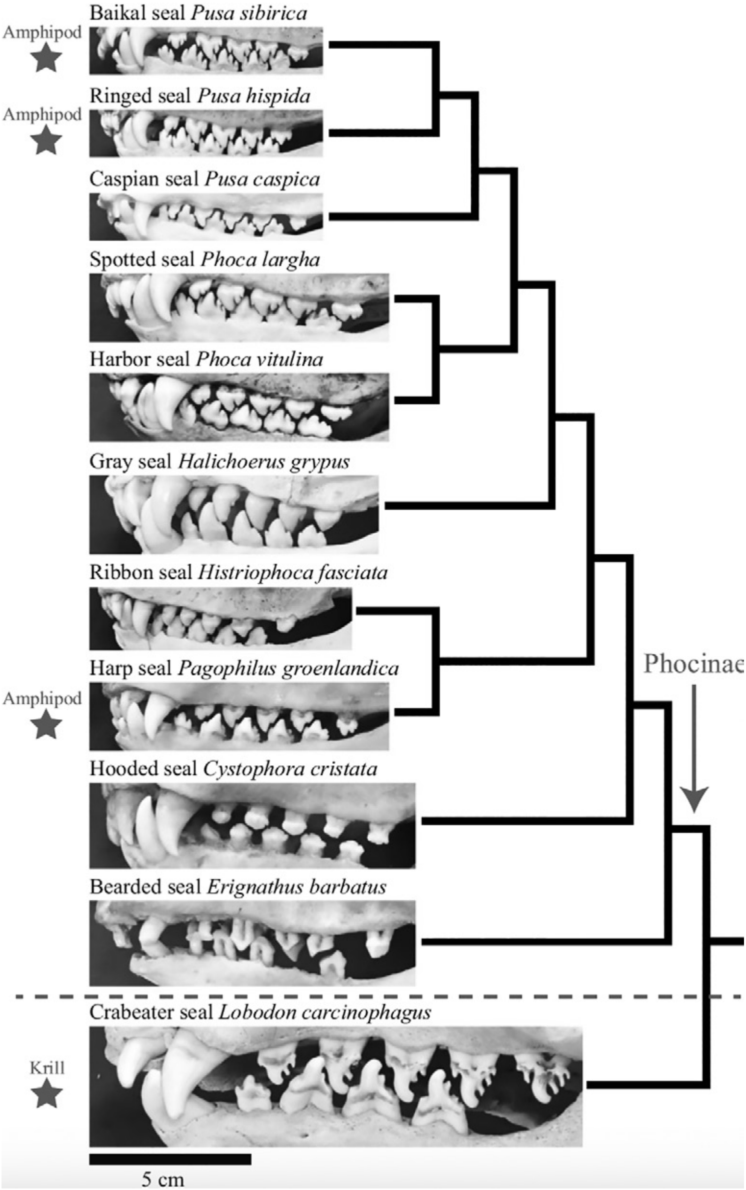
of fifty-seven *Macrohectopus* per dive, with each dive lasting about ten minutes. This led to the consumption of sometimes thousands of these gammarids per day.

Hunting was so efficient in part because the seals followed the vertical migrations of their prey, feeding on the gammarids mainly at night when they are shallower. In addition, they tracked the dense layer of migrating gammarids as it moved over the course of the evening and even during a single dive (figure 8.6). This highlights the pace and synchrony of these migrations.

Nerpa may also be aided in their high-speed snapping up of tiny prey by teeth that appear to be specialized for this purpose (figure 8.7). Like a few other seal species that feed on open water crustaceans, nerpa have comblike postcanine teeth. These likely allow the large amounts of water taken in during rapid foraging to be efficiently expelled while retaining prey.

The convergence with crabeater seals, which forage on krill in Antarctic waters, is especially striking, as is the contrast between the teeth of the nerpa and those of the closely related Caspian seal, which does not feed on amphipods. It remains to be seen if nerpa can suck in prey at a distance, as crabeater seals can. A captive crabeater was observed to suck in prey from half a meter!

Watanabe and colleagues suggest that the nerpa foraging on gammarid amphipods, rather than on the fish that eat the amphipods, has important ecosystem implications as well as for the nerpa. By eating lower on the food chain, the nerpa can take advantage of higher prey abundance owing to the energy that would have been lost in the transition from amphipods to fish. This may help to explain the exceptional abundance of nerpa in a deep, cold, unproductive lake; nerpa densities are several times higher per square kilometer than the densities of Caspian seals or two other freshwater seal populations. The nerpa's ability to survive and maintain high densities in a stressed, limited environment by eating lower on the food chain may carry a message for us too. Our odds of lasting a little longer in our own stressed, high-density habitat will likely be higher if we move down the food chain a link or two.


Baikal seal Pusa sibirica
Amphipod
Ringed seal Pusa hispida
Amphipod
Caspian seal Pusa caspica
Spotted seal Phoca largha
Harbor seal Phoca vitulina
Gray seal Halichoerus grypus
Ribbon seal Histriophoca fasciata
Harp seal Pagophilus groenlandica
Amphipod
Phocinae
Hooded seal Cystophora cristata
Bearded seal Erignathus barbatus
Crabeater seal Lobodon carcinophagus
Krill
5 cm

THE ABYSS: DESERT AND OASIS

Baikal's sponge forests are distinctive and beautiful, and its open water food chain is like no other. But among freshwater lakes, its most unique feature is its abyss.

Oxygen levels in the deepest areas of Baikal are often slightly lower than at the surface, but a great deal higher than in the depths of other ancient lakes and more than sufficient to support mature fish, amphipods, and other large invertebrates. Light from the surface, however, is almost absent below about 400 meters, meaning there is no photosynthesis and most food, which is sparse, must come from above. Temperatures are relatively constant, from about 3.2 to 4.0°C. Thus, the environment is stable, if difficult.

In the abyss, below about 400 meters, Baikal's fishes are all endemics and all sculpins. Other fish just do not go so deep, with pressure being one important reason. The majority of sculpin species occupy a wide depth range, including shallower waters that receive natural light and at least some of the deep, dark waters; about nine species are confined to shallower waters and do not venture into the abyss. About six bottom-dwelling

Figure 8.7

The jaws and teeth of the nerpa and other seals, with feeding on krill or amphipods indicated, and their relationships. Note how different the Nerpa's teeth are from those of the closely related Caspian seal. *Source:* Reprinted with minor modifications with permission of the National Academy of Sciences of the USA, © 2020, National Academy of Sciences, from Watanabe et al., "Ultra-high Foraging Rates of Baikal Seals Make Tiny Endemic Amphipods Profitable in Lake Baikal," *Proceedings of the National Academy of Sciences* (2020).

species (i.e., excluding the golomyankas of open waters) live overwhelmingly below 400 meters, including two that are generally found below 900 meters. In their authoritative overview of Baikal's biodiversity, Kozhova and Izmest'eva provide an unappealing portrait of these deepwater sculpins: "[They have] a flabby body, covered with a tender skin easily gathering in folds . . . [and their] eyes are mostly reduced. The body is colorless or light pale-yellow and, as a rule, there are no spots." In the gammarids, the vast majority of species are either native to shallow waters or can live in a wide range of depths. The number of species found in the abyss is small, and the number found there exclusively is smaller still. Kozhova and Izmest'eva describe some common features of the abyssal species: "[The] eyes . . . lack pigmentation or are pale pink, but their antennae, as a rule, are very long. Body coloration is usually whitish or pinky-white."

Other Baikalian invertebrate radiations are less well studied than the gammarids, but are known to be represented in Baikal's dark depths. These include annelid worms, among them *Tubifex* sp., which are related to the worms sold as live food in aquarium shops, and planarian flatworms that include a set of frequently carnivorous deepwater species up to thirty centimeters in length. For those of us who know planarians as tiny creatures sometimes used in biology teaching laboratories, usually with an emphasis on their remarkable regenerative abilities, these large predatory worms are a bit nightmarish. If their regenerative capacities are like those of their smaller relations, they would seem a perfect model for a horror movie creature, and indeed they sit surprisingly high on the food chain. There are also sponges, snails, and copepod crustaceans. At a smaller scale, numerous undescribed nematode worms await study, as they do in many habitats; ostracod crustaceans, or seed shrimp, are notably diverse as well.

The abyssal denizen that is perhaps most surprising is an insect. It is quite ordinary to find insect larvae in streams and lakes, but finding them under more than a kilometer of water, which they must somehow safely traverse to metamorphose into adults and reproduce, is unexpected to say the least. Yet in the stygian recesses of Baikal, where for millions of years sunlight has been a rumor from afar, and the difference between a blistering July and the most numbing January is a fraction of a degree, one can find the larvae of chironomid midges. These are not exotic beasts like a horror movie flatworm or a golomyanka but instead prosaic little creatures that are related to the "bloodworms" commonly sold as frozen food for aquarium fish.

Most of the deepwater denizens of Baikal get their nutrition from the rain of dying, dead, and decaying organic matter that emanates from productive waters closer to the surface, just as do many deep-sea creatures. Thus, the depths are in most places something of a desert, though really there is no terrestrial habitat that provides a satisfactory analogy. Even in a desert there are cacti or other organisms that manage to perform photosynthesis and provide a foundation for a food chain. In the deep, there is just that slow rain and the occasional bonanza of a dead sturgeon or maybe a seal, likely to be quickly pounced on by specialized scavenging gammarids with keen senses for the detection of such prizes.

Except . . . just as in the deep sea, in Baikal one can sometimes find a source of energy and carbon that comes from below. Baikal has hydrothermal vents and methane seeps, and these are the basis for higher-density animal communities, much like in the ocean. So far, there do not seem to be any Baikalian equivalents of the tube worms and bivalves of deep-sea vents, which have chemoautotrophic (i.e., extracting energy from the materials flowing from the vent, without photosynthesis) bacteria living symbiotically within them, but there are free living bacteria that similarly form the basis for food chains. This is not completely unprecedented in fresh water. For example, there are vents in Lake Tanganyika that are associated with communities of microbes, but any such communities in the abyss of Tanganyika would be in waters that generally lack oxygen. Hence persistent animal communities around deepwater vents would not be possible.

The study of Baikal's vent and seep communities only got started in the last few decades as deep-diving minisubmarines became available for the direct exploration of the lake's deeps. Exploring Baikal's unknown abyss in a minisub sounds like a fantasy come to life for anyone who grew up watching Jacques Cousteau and similar programs, as many of us did. But apparently these trips require fortitude. A colleague of mine who has made descents in the Atlantic reported how tight the confines were, with two or three people crammed together and no bathroom facilities. On one trip some years back, one of the scientists developed digestive tract problems; since there is great reluctance to interrupt these expensive excursions and the ascent can easily take a few hours regardless, the atmosphere in the sub became rather thick.

The advantage of the subs is that direct, recorded observations can be made of the environment around the sub, and carefully selected samples, including live animals, can be collected

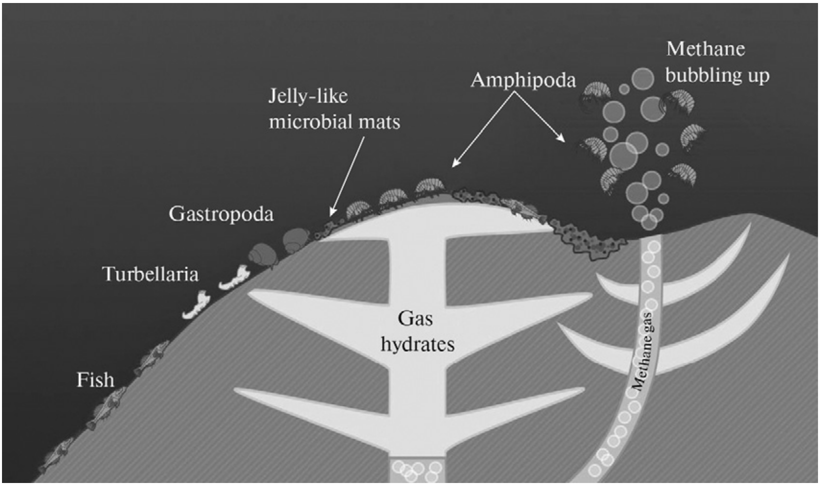


Figure 8.8
"Saint Petersburg" Baikal methane seep community. *Source:* Reprinted with minor modifications with permission from Springer Nature, from Sitnikova et al., "Trophic Relationships between Macroinvertebrates and Fish in St. Petersburg Methane Seep Community in Abyssal Zone of Lake Baikal," *Contemporary Problems of Ecology* (2017).

with slurp guns, sediment corers, and other devices. The video observations have revealed otherworldly environments quite different from the flat, deep sediment that otherwise dominates the bottom of Baikal.

At the Saint Petersburg methane seep, about 1,400 meters below the surface in the central portion of Baikal, the bottom landscape is small hills of four to six meters in height (figure 8.8). These are composed partly of ice-like, transparent blocks of gas hydrate, which are best known from the deep sea. In the ocean, they sometimes form where methane bubbles up under the terrific pressures and low temperatures of deep water. At

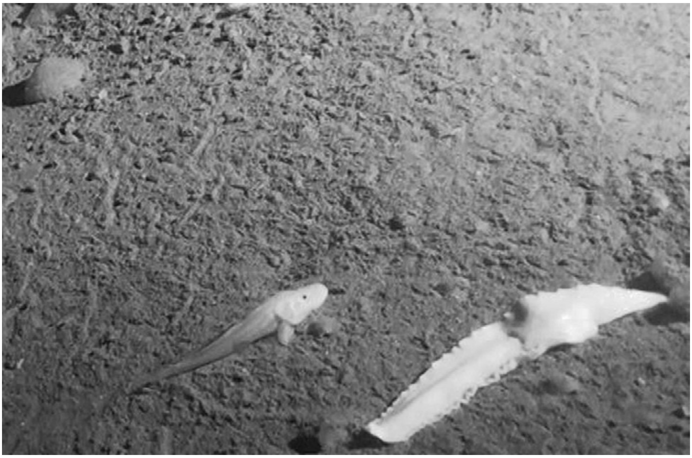


Figure 8.9
The abyssal sculpin *Abyssocottus korotneffi* alongside a giant planarian of the Dendrocoelidae at Baikal's Saint Petersburg methane seep. *Source:* Reprinted with minor modifications with permission from Springer Nature, from Sideleva, "Communities of the Cottoid Fish (Cottoidei) in the Areas of Hydrothermal Vents and Cold Seeps of the Abyssal Zone of Baikal Lake," *Journal of Ichthyology* (2016).

other sites, small, gurgling mud volcanoes may occur, or hillocks and tubes of bitumen, essentially an oily tar.

Mats of bacteria are common at these lake-floor oases and likely form the basis for the food chains. Many of the organisms generally characteristic of abyssal Baikal are present at these sites, though in much-elevated numbers. Thus, there are sponges, sculpins, planarian worms, annelid worms, gastropods, chironomid midge larvae, and others. Large flatworms are often notably common (figure 8.9).

While the species present overlap extensively with those of the surrounding lake-floor desert, the relative abundances of individual species, which are best known for sculpins and gammarids, may be different. They may also differ between seeps and vents. Among the sculpins at the Saint Petersburg methane seep, for example, Valentina Sideleva of the Russian Academy of Sciences reports that *Neocottus werestschagini* is the most common species. This species, however, is infrequently encountered on the lake bottom generally, or about fourteen times less often relative to other species, than at the seep. At the Frolikha Bay hydrothermal vents, located in 400–480 meters of water, a species of the same genus was overwhelmingly dominant, but this time it was *Neocottus thermalis*, a more extreme specialist in that it is only found at hydrothermal vents and is the only sculpin known to possess such an exclusive affinity. It has no obvious adaptations that restrict it to the vents so the reason for this inflexible association remains unknown. The two golomyanka species are also notably abundant at both the vent and seep sites. Up to fifteen individuals could be seen in a single video frame taken at the vent, and thirty at the seep. They were therefore several times more abundant than they are in the open lake. This pattern too is a puzzle, as they are not feeding on vent or seep organisms; instead, they are sometimes eaten by the bottom-dwelling sculpins that are abundant there.

By examining the carbon and nitrogen isotopes present in the organisms dwelling at the seep, Sideleva and a group of Russian colleagues from several institutions were able to infer whether seep organisms' nutrition originated with seep microorganisms or came from a food chain that began with photosynthetic production closer to the surface. They found that many of the bottom-dwelling sculpins, gammarids, and planarians appeared ultimately to be deriving most of their energy and carbon from the seeps. Similar results have been obtained for vent systems, although in contrast to the bottom-dwelling sculpins, golomyankas were found to derive their nutrition from the open water ecosystem, where most energy originates with photosynthesis near the surface. None of these analyses have identified any organisms that appear to be hosting symbiotic bacteria that are generating energy and carbon compounds. But all conclusions for these systems are still based on small samples. Surely there will be many more surprises coming, especially as exploration expands through the use of less expensive, remotely controlled underwater drones.

BAIKAL IN THE ANTHROPOCENE

The final chapter of this book is focused on the accelerated pace of change lately confronting ancient lakes, as our species comes to dominate this unusual little planet ever more exhaustively. Yet it would seem incomplete to depart from Baikal without saying a few words about the developments there during the last decades, particularly since they encompass major features of its massive ecosystem. Processes in Baikal are also somewhat special because although there are other ancient lakes at high latitudes, especially if one uses Stephanie Hampton and colleagues' definition, Baikal is the highest-latitude ancient lake with extensive endemism, and the only such lake covered in ice each winter.

As the largest and deepest of freshwater lakes, with a vast volume comprising 20 percent of the planet's liquid fresh water, one might expect Baikal to be resistant to change. Thus, there was a good deal of interest when comprehensive analyses began to appear in the 2000s of the sixty-year data sets collected by Kozhov, Kozhova, and Izmest'eva. These and other data show clearly that Baikal is warming and that the annual duration of ice is shrinking (figure 8.10). It is also becoming apparent that these changes are affecting the lake's organisms indirectly through effects on other physical processes in the lake as well as directly. In some cases, changes in physical processes are affecting how organisms interact with each other.

In the first major report presenting comprehensive analyses of the data collected by the Kozhov family, Hampton, of the US National Center for Ecological Analysis and Synthesis (now at the Carnegie Institution for Science), Izmest'eva, and a team of collaborators from multiple institutions reported on the biological changes that had accompanied the warming of Baikal. They found that algal mass has been increasing overall, as have the numbers of a group of widely distributed zooplankton known as cladocerans, which do well at higher temperatures. In contrast, the endemic, cold-loving *Epischurella* has been either declining slightly or stable. Owing to physiological and other differences between the different types of zooplankton, Hampton, Izmest'eva, and colleagues suggest that if these trends persist or intensify, patterns of nutrient cycling in the lake could be substantially affected, with broad ecological consequences.

In a complementary analysis of data from shallow sediment cores, an international team led by British scientists George Swann (University of Nottingham) and Anson McKay (University College London) looked at how natural and human-driven

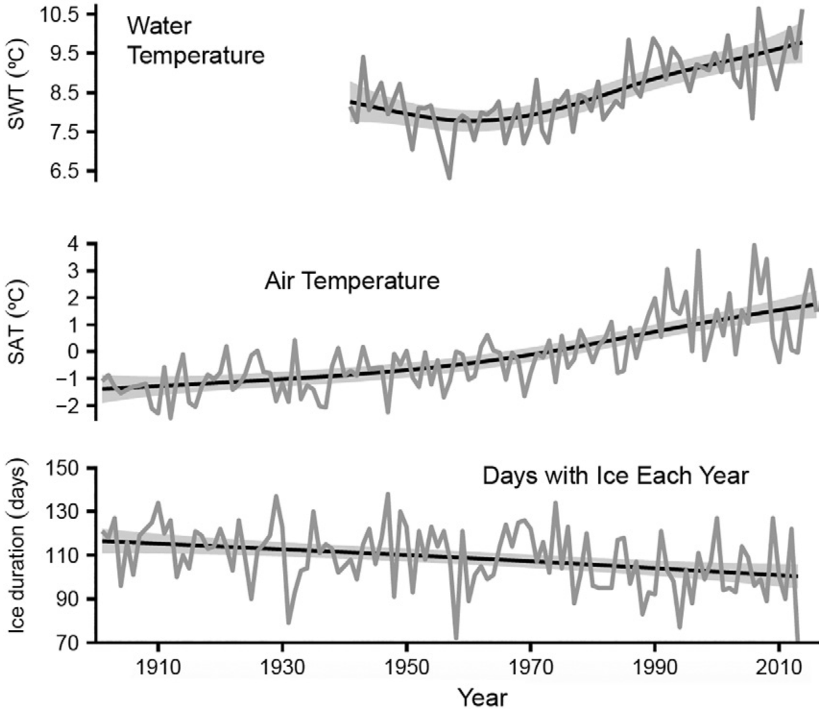


Figure 8.10

Temperature and ice cover trends at Baikal. *Source:* Reprinted with minor modifications from Swann et al., "Changing Nutrient Cycling in Lake Baikal, the World's Oldest Lake," *Proceedings of the National Academy of Sciences* (2020). Published under a Creative Commons CC BY 4.0 license (https://creativecommons.org/licenses/by/4.0).

changes have affected nutrient and chemical cycling, and ultimately changes in algae productivity. Their time frame of 2,000 years was longer, but still comparatively recent. Their most important conclusion is that since the mid-nineteenth century, the supply of key nutrients has greatly increased, from the nutrient-rich deeper waters to the nutrient-limited shallower waters where light is high and algae can be productive. They suggest that this is the result of documented increases in wind strength over the lake, which can cause more extensive "ventilation" of deep waters. The cause of increased wind strength is not yet known with confidence, but decreased ice cover along with increased air and surface-water temperatures likely contribute.

Hampton and Izmest'eva have built on these and other findings in a mathematical model of the Baikal open water ecosystem, developed with several additional collaborators including Sabine Wollrab of Michigan State University and Berlin's Leibniz Institute of Freshwater Ecology and Inland Fisheries. In the model, they seek to integrate biological interactions between organisms with changes in the physical environment. Their goal is to better understand the causes of the recent changes in seasonal patterns of algae abundance, especially in the winter. Baikal, with sunlight penetrating its clear winter ice, has traditionally had a peak in algae productivity in the winter and early spring—yet another unusual feature of this system. In the late twentieth century, these peaks were often delayed, weaker, or simply absent. The Kozhov family's data detected these patterns, which can seldom be evaluated in lakes, because of their determined sampling through the winters. The model, which takes into account *Epischurella* abundance and grazing, and considers separate populations of cold-adapted and warm-water-adapted algae, suggests that these changes in algae abundance may be largely the result of reduced annual ice cover and that if ice coverage continues to diminish the winter algae peak may disappear altogether. The model is somewhat complex, but its predicted outcomes arise at least in part from the greater ability of the *Epischurella* to suppress algae population growth by eating the algae when there is less ice cover. The model describes a "regime shift," a steplike switch from one state of a system to a different state involving a different range of variation. No model is final, and this one may evolve as our understanding of the ecological interactions evolves, but the contrast between regime shift and steady, gradual change is worrisome and even frightening. It indicates that global warming and other human-generated environmental changes may sometimes cause abrupt shifts in ecosystems that may be hard to both predict and reverse.

* * *

Lake Baikal, the largest and most ancient of freshwater ancient lakes, had its start in the time of the dinosaurs and began to take its modern form well before the appearance of our own lineage, the Homininae. Yet it only assumed its current deep and thoroughly oxygenated character in the late Pleistocene. Among its diverse endemic fauna, its gammarid amphipods and sculpins are especially well studied. Species from both radiations are uncharacteristically important in open water food chains, and also as prey for the planet's only species of freshwater seal, the nerpa. Other gammarid and sculpin species are important in

Baikal's highly distinctive abyssal vent and seep communities. As the biodiverse ancient lake at the highest latitude, Baikal is showing the direct and indirect effects of global warming on its physical and biological systems and processes. The lake may be experiencing an ecological regime shift that should give pause to creatures living in a larger yet still finite ecosystem—one that is quickly heating too.

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A Natural History

By: Jeffrey McKinnon

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