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Resiliency and Collapse: Lake Trout, Sea Lamprey, and Fisheries Management in Lake Superior

Nancy Langston

Michigan Technological University, nelangs3@mtu.edu

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Border Flows: A Century of the Canadian-American Water Relationship

Heasley, Lynne; Macfarlane, Daniel

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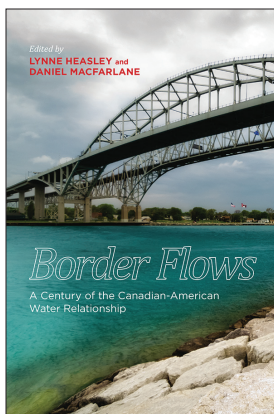
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Edited by Lynne Heasley and Daniel Macfarlane

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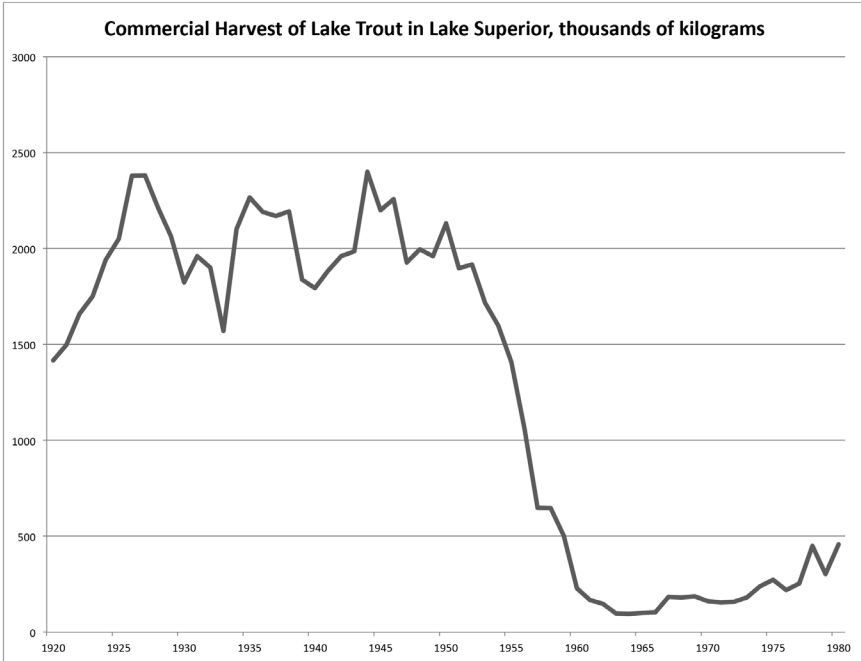
Resiliency and Collapse: Lake Trout, Sea Lamprey, and Fisheries Management in Lake Superior

NANCY LANGSTON

Just as quick as they began to clear the country up the fish began to disappear.

—John Barret Van Vlack, Georgian Bay fisher, 1894¹

Lake trout (*Salvelinus namaycush*)—voracious predators at the top of Great Lakes food chains—sustained a tribal and commercial fishery in Lake Superior for centuries. Even after other fish populations crashed under commercial fishing pressure, pollution, and habitat loss, lake trout appeared surprisingly resilient. But in the mid-twentieth century, their populations fell off the edge of a cliff (see Figure 1). In 1944, the commercial catch of lake trout in Wisconsin alone totalled more than six million pounds; a decade later, only a few fish were caught, and by 1956, lake trout had vanished from most of the Great Lakes. Having been top predators, the loss of lake trout had rippling effects. Populations of rough fish such as alewives and smelt exploded when their predators vanished, and zooplankton



8.1 Lean lake trout harvests, 1920–1980. Data courtesy of R.E. Hecky et al., *Global Great Lakes*.

populations dropped sharply.² When commercial and tribal fisheries shut down, leaving local economies with little to support them, the social effects were devastating.

Why did lake trout crash so suddenly? For decades, fisheries biologists have placed most of the blame on the sea lamprey (*Petromyzon marinus*), which the U.S. Geological Survey calls “a marine invader from the Atlantic Ocean” that “quickly devastated the fish communities of the Great Lakes.”³ The historical narrative offered by fisheries biologists is that sea lamprey invaded the upper Great Lakes after modifications to the Welland Canal allowed marine organisms to make their way upstream past Niagara Falls. Sea lampreys sucked the fluids from lake trout, soon devastating their populations. Eventually, chemists and fisheries biologists managed to restore lake trout with the help of TFM, a synthetic chemical that kills developing lampreys without hurting too many young lake trout.⁴

This story has satisfied many folks, perhaps because it essentially takes the blame off people. Yes, people did modify the Welland Canal in this story and open the Pandora's box of invasive species. But they did not intend to do this, and anyway, scientists saved the day. The problem is that the evidence supporting this story is equivocal at best. Sea lampreys did indeed parasitize a lot of lake trout, but it is not clear that the sea lamprey really were non-native invaders that snuck into the upper Great Lakes and then wiped out their hosts. Nor is it clear that lake trout would have been fine if only the sea lamprey had not shown up. Intensive harvests, toxic chemicals, and loss of habitat had already stressed fish populations in the Great Lakes before the lamprey invaded. Most frustrating for the sea lamprey hypothesis, controlling sea lamprey populations has failed to restore breeding populations of lake trout in most of the Great Lakes. This chapter argues that while sea lamprey were an important factor in the collapse of lake trout populations, focusing on them alone ignores the larger context of ecological change and restoration in the Great Lakes.

Lake Trout

Lake trout, a huge freshwater char, were once present in enormous populations within the Great Lakes. Slow growing, they typically become sexually mature at seven to ten years of age, making their populations vulnerable to overfishing. In the Lake Superior basin, biologists identify two different subspecies of lake trout—the lean lake trout and the siscowet lake trout—and two additional varieties (humpers and hybrids). Both varieties are fond of eating other fish, particularly whitefish. This puts them near the top of the food chain in Lake Superior, making them vulnerable to chemical bioaccumulation. Toxic chemicals found at very low levels in water become concentrated by orders of magnitude as they make their way up food chains.

Historically, siscowet lake trout made up most of the lake trout biomass in Lake Superior. Siscowet prefer very cold, very deep water; they live their entire lives in waters colder than 4°C, and as adults, they spend much of their lives at depths greater than 150 metres. Their fat content is extremely high—from 30 percent to 90 percent by weight—which means they are well adapted for the coldest depths of Lake Superior.⁵ Lean lake

trout have much lower fat content than the siscowet and tend to be smaller, live shorter lives, and spawn in shallower waters.

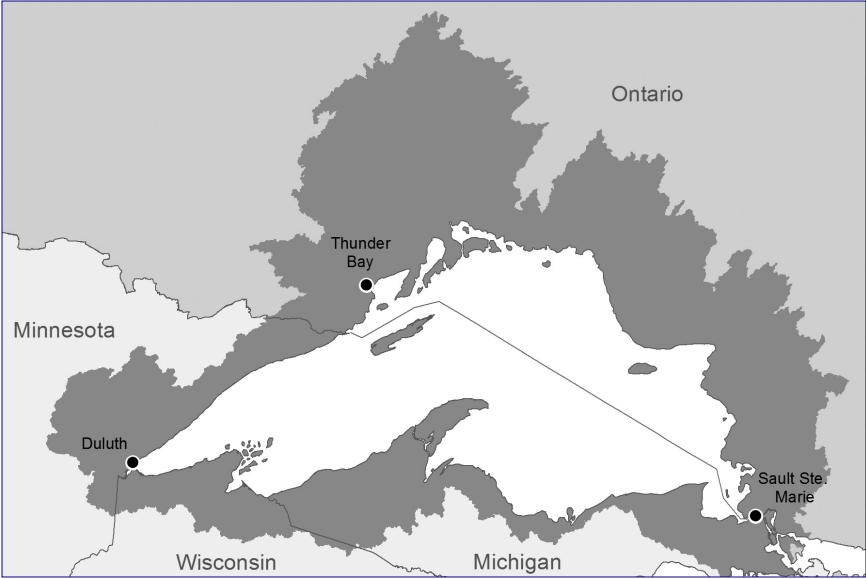
Early records note that, like whitefish and coaster brook trout, lean lake trout and siscowet could spawn in rivers (siscowet also spawned on offshore reefs). Unlike coaster brook trout, whose populations declined after logging and dam-building reduced their access to good stream spawning habitat, lake trout populations were resilient enough to adapt to the loss of tributary spawning habitat.⁶ Lean lake trout spawned in shallow, near-shore habitat less than thirty metres deep, preferring spawning reefs that were washed clean of sediments by flowing lake currents. Both lean and siscowet subspecies returned to spawn at the place where they were born.

Lake Superior Overview

Lake Superior lies at the head of the Great Lakes Basin, which contains about 21 percent of all the fresh surface water on the planet (Figure 2). Water from the Great Lakes provided power, transportation, and a convenient sewer for late-nineteenth-century industrialization.⁷ While few of those factories or cities were located in the Lake Superior portion of the basin, the effects of local pollution discharges were intensified by the fact that in Lake Superior, only about 0.5 percent of the lake's water turns over each year. A drop of water that enters Lake Superior takes, on average, 191 years to leave the lake.⁸

Lake Superior is a big, deep lake. Its surface area is the largest of any freshwater lake in the world: 82,103 square kilometres—which, *Wikipedia* helpfully tells us, is approximately the size of South Carolina. At its deepest, the lake is 406 metres deep with an average depth of 147 metres. For comparison, Lake Erie, the shallowest Great Lake, averages only 19 metres deep.⁹ Lake Superior is big enough to swallow all the other Great Lakes, with room left over for three additional Lake Eries. Put another way, there is enough water in Lake Superior to cover all of North and South America in a foot of water. The Canadian Shield's thin soils and high resistance of rocks to weathering helps Lake Superior to remain clear, biologically unproductive, and slow to accumulate sediments.¹⁰

Lake Superior is also very cold, with an average annual temperature of 4°C (39°F). Cold waters shape its ecology in profound ways. Like a few



8.2 Lake Superior basin. Map by Jason Glatz.

other cold, deep lakes, Lake Superior is ultra-oligotrophic, meaning that it is quite low in productivity (i.e., aquatic plant and algae production) and high in dissolved oxygen. In the summer, surface temperatures rise while temperatures below 200 metres remain at 4°C, and this variation in temperature stratifies the lake into three distinct layers: the epilimnion (the uppermost, warmest layer); the metalimnion or thermocline (the middle layer, which may change depth during the day); and the hypolimnion (the deepest, coldest layer). Twice each year the water column reaches a uniform temperature from top to bottom and the waters mix.¹¹

In most lakes, fish rarely use the hypolimnion, because when organic matter decays, oxygen gets depleted down in the deepest layers of the lakes. However, in large, oligotrophic, stratified lakes such as Lake Superior, low nutrient levels mean that populations of algae (and the animals that feed on them) remain low, so the water remains clear and dissolved oxygen levels remain high all the way down to the bottom. Lake Superior's coldness and lack of productivity means that siscowet lake trout, which need substantial concentrations of oxygen, can thrive in the hypolimnion, so deep that fishermen find it hard to reach them, giving the fish a measure

of resiliency even when fishing pressures are quite high. But the particular ecological conditions that make Lake Superior excellent habitat for lake trout—cold, clear, and clean—also make it vulnerable to tipping over thresholds of sudden environmental change, such as a warming climate. If conditions warm, lake levels decrease, or nutrient levels increase, the hypolimnion may become depleted of oxygen, depriving cold-water fish of necessary habitat. Lake trout fisheries are therefore sensitive to anything that increases temperature or inputs of organic matter.¹²

Considering its enormous surface area, the lake's watershed is relatively small, which has historically helped minimize the contaminants that wash off the land into the water. But fewer sources of contaminants from the watershed have not always meant better water quality for fish, for two main reasons. First, the long retention time of Lake Superior means that a drop of water (and an associated contaminant) that enters the lake may remain there, on average, for nearly two centuries.¹³ Second, the cold temperatures of the lake and the structure of the lake bed mean that once contaminants enter Lake Superior, they may stick around near the shore for a long time, where fish can easily encounter them. In the spring, the nearshore waters of Lake Superior heat up more quickly than the deeper offshore waters. Because warm water is less dense than cold water, a thermal bar forms at the convergence of the nearshore water and the colder, denser, offshore water. This early-season concentration of nutrients promotes primary production in the nearshore area, accelerating the establishment of warm, eutrophic conditions along the shoreline. The thermal bar also acts as a barrier, concentrating floating debris, warm water discharges, and pollutants within the nearshore area.¹⁴

Because of Lake Superior's geographic position on the Canadian Shield, lake depths sharply increase quite close to shorelines. This means that shallow, nearshore habitat (which is required by lean lake trout) is rare on the lake. Unlike Lake Erie, for example, where most of the lake is shallow, warm, and productive, only 20 percent of Lake Superior's area consists of nearshore open water habitat (technically defined as areas where the water is less than 80 metres deep). In the nearshore, waves and current scour sediment from the substrate, maintaining good spawning and nursery habitat for many fish species while also providing excellent habitat for many aquatic invertebrates.¹⁵ The relatively small area of nearshore habitat in Lake Superior means that fish that spawn in the nearshore habitat—such

as lean lake trout—are particularly vulnerable to toxics held close to shore by the thermal bar in spring.

Why does all this biophysical detail matter? While fishermen often paid close attention to the physical details that helped them catch fish, regulators and planners in the basin often ignored biophysical complexity. In the late nineteenth and early twentieth century, towns such as Port Arthur (now Thunder Bay) were not oblivious to the potential problems of urban development and pulp mill pollution in the lake. They knew that their drinking water usually came from the lake, and they also knew that the commercial fishing industry might collapse if pulp mill waste killed too many spawning fish. Early pollution discussions, however, tended to assume that the lake was one homogenous body of water. If you dumped a few gallons of toxics near the shoreline, surely that would quickly be diluted by the vast quantity of water in the lake.¹⁶

Yet Lake Superior's enormous size, which made planners hope that dilution might be the solution to pollution, actually worked against them. Lake Superior is large enough and cold enough that when thermal bars form, they hold pollution close to the nearshore; it concentrates there and makes its way into sediments or into the water column and, from there, eventually into the bodies of large predatorial fish—and of those who eat them. Fish also refuse to distribute themselves uniformly throughout the lake. They experience the lake as a complex set of interconnected ecosystems. During certain periods of spawning and fry development, they take refuge in the same places where pollution gets concentrated. Pulp mills and towns tried to manage pollution as simply and cheaply as possible, but their models did not account for the complexity of nearshore habitats, limnological conditions, bumpy shore bottoms, shoals that catch currents carrying sediments, or fish with minds of their own.

Watershed Changes

Changes to Lake Superior watersheds began long before industrialization intensified in the late nineteenth century. After the glaciers retreated, forests developed along the shores of the lake. These forests were neither stable nor uniform; they ebbed and flowed with fires, insect outbreaks, windstorms, and human pressures. Between twenty-five and ten thousand years

ago, the Wisconsin glaciation shaped the physical geography of soils that still serve as a key template for today's forests. When the glaciers retreated, cold lingered, and forests were slow to move in. About seven thousand years ago, as the climate warmed, people, pines, and hardwoods migrated into the region. Three thousand years ago, the climate cooled again and precipitation increased, leading to rippling changes in basin forests; hemlock invaded pine stands on rich, loamy soils in the southern portion of the watershed, while pines, aspen, and birch persisted on sandier soils and a boreal forest covered the northern shore.

As people came, they changed the watershed. Changes on the land had significant impacts on aquatic habitat, especially in the nearshore environments where lean lake trout spent most of their lives. While quantifying these land-use effects on fish populations is difficult, if not impossible, it is important to recognize that they were key stressors in fish changes.

Mining was one of the key ways that people—both Indigenous and of European ancestry—made a living along the shores of Lake Superior. Copper ore-refining processes required huge amounts of water for the stamping mills. Water was returned to the lake contaminated with particles of copper-bearing tailings that filled bays, harbours, and inland lakes. By 1882, stamp mills were dumping about 500,000 tons of stamp sands into local waterways each year. The Keweenaw Peninsula near Hancock and Houghton was soon deforested to fuel the copper smelters and remained bare for three-quarters of a century.¹⁷

Iron mining changed fish habitat as well. In the mid-1840s, the first of the iron ranges in the Great Lakes drainage basin came into production near Marquette, Michigan. Iron tailings were often less toxic than copper tailings, but the refining process added significant quantities of mercury to the watershed, soon becoming an important source of mercury in the lake. Some iron mines were vast open pits, while others were deep shaft mines; both led to significant changes in fish habitats. Miners sliced off forests and the soils that sustained them to create the open pit mines, leading to increased runoff and siltation in tributary streams. Deep shaft mining pumped groundwater to keep the mines dry, lowering the water table and creating silt-filled runoff. Timber shored up shaft tunnels in deep mines, while the smelting furnaces demanded timber. By 1903, for example, the iron furnaces of the Upper Peninsula consumed thirty acres of hardwood forest a day, every day of the year.¹⁸ Mining-related runoff led to increased

siltation that covered spawning beds, raised water temperatures, and changed river flows.

Loggers on the American shores of Lake Superior between 1890 and 1910 created new disturbances, the scale of which dwarfed that of earlier ones. By 1898, the federal forester Filbert Roth estimated that only 13 percent of the white pine was still standing. Roth wrote that deforestation had made “decided changes in drainage and soil moisture,” diminishing the flow of larger rivers. Swamps had dried up, while hardwood thickets replaced wetland forests.¹⁹ Log drives scraped streambeds clean, spring dams destroyed riparian habitat, and dams for logging blocked the passage of fish upstream for spawning. Sawmills dumped vast quantities of sawdust and wood scrap into nearshore estuaries and rivers. The sawdust floated on the surface and then became waterlogged and sank, clogging harbours, covering spawning and feeding grounds for fish, and filling in the critical nearshore estuarine habitat. Large quantities of sawdust on the shallow bottoms could consume enough oxygen to kill fish.²⁰

As forests fell, farms briefly replaced them. The geologist Faith Fitzpatrick’s research suggests that, along the clay plain of Wisconsin’s south shore, erosion from farming dwarfed the contribution from logging. Nutrients bound to sediments moved off the farmland into the estuaries and streams, lowering levels of the oxygen critical to fish reproduction and adulthood. Clear bottoms became smothered with silt, which harmed spawning of cold-water fisheries (and later offered a perfect habitat for developing sea lampreys).²¹ Many contemporary observers were concerned that stream flow seemed to change after logging and farming, with floods and erosion becoming more common, as well as late summer drought.²²

On the Canadian shore, except for isolated logging of white pine along the north shore for shipbuilding, and near Thunder Bay for paper-industry development, relatively little logging took place until World War I.²³ After the war, the Canadian government encouraged industry partnerships to develop towns around enormous pulp mills on the shores of Lake Superior. Government and industry partnership infused funds into the region to develop the tremendous fibre resources of the boreal forests, particularly the long, thin fibres of black spruce. The Anglo population in northern Ontario soared, drawn by company-built towns with inexpensive housing and good jobs in the mills.

Pulp mill development depended on abundant sources of cheap water. Water was critical for transportation, pulp processing, and power to run the mills. Entire rivers were diverted from one watershed to another, in part to provide hydropower for the pulp industry (see chapter 4 in this volume). Above all, water was essential for disposal of toxic effluents. As early as 1894, contemporary observers expressed concern about pulp mill pollution, noting that the Alpena Sulphite Fiber Company produced acid waste that drained directly into the local river; according to Casper Alpern, a local fish dealer, that waste was “poison to the fish.”²⁴ Yet to planners, as mentioned earlier, Lake Superior seemed like a reasonable place to dump toxic wastes from the mills. Dilution is the solution to pollution, experts reasoned. Their models predicted that Lake Superior could handle the effluents from pulp production, including high levels of mercury, PCBs, and phenolic acids from the natural plant chemicals, which were unnaturally concentrated in pulp processing.²⁵ Moreover, while urban planners worried about human health and drinking water, they believed that bacterial diseases were most significant. It seemed much cheaper to filter and treat bacterially contaminated waste for human use with chlorine (which harmed fish) and hope that the natural waters would dilute most pollution.²⁶

For a generation, pulp and paper towns boomed along the Canadian shore. Marathon, Terrace Bay, and Thunder Bay all relied on an industry made possible by the perception that pulp and paper production made the best use of boreal forests, that logging increased water yield from forests, that lake water was best devoted to industrial development, and that pollution would be so diluted by the abundance of water in Lake Superior that it could not harm fisheries or human health.

Fishing

People had begun fishing in the Lake Superior basin as soon as the glaciers had retreated.²⁷ By 3000 to 2000 BCE, Indigenous peoples had adapted a broad range of fishing technologies to the conditions they found in the Great Lakes, using spears, gaffs, hooks and lines, and weirs in Lake Superior. In the lower Great Lakes, they had begun using nets about 2,500 BP, but in Lake Superior, net fishing did not begin for at least another two

thousand years (sometime between 300 and 200 BP).²⁸ Well into the twentieth century, these core technologies remained at the heart of the fishery: what changed, however, were the new national and global markets that drove expansion of harvests.

From the 1600s to the 1800s, French exploration, the fur trade, and wars created market pressures that led to intense extraction first of beaver and then of fish.²⁹ When beavers were removed from much of the watershed, stream patterns changed, wetlands eroded, and nearshore fish habitat diminished.³⁰ The fur trade created new markets for fisheries, with the American Fur Company establishing a commercial fishing industry on Lake Superior in the 1830s. The goal was not to feed the traders themselves, but to replace corporate income that had diminished as the beaver were depleted. In 1837, the company shipped two thousand barrels of combined lake trout and whitefish; in 1838, four thousand barrels were shipped, and in 1839, five thousand were shipped. For comparison, this means a peak harvest of about one million pounds—which is a lot of fish. In fact, it is slightly less than a sixth of the highest yield between 1941 and 1950 of lake trout and whitefish combined, an average yield of 5.8 million pounds.³¹

How many lake trout did Lake Superior support before the advent of land-use change and commercial fishing? And when did those populations change? It is impossible to state with certainty the pre-nineteenth-century fishing populations of lake trout in Lake Superior. Descriptive archival records stress their abundance—but people exaggerate, particularly when they are writing home about the natural wealth they have stumbled upon. While these anecdotal records can suggest presence or absence and also give a sense of abundance or rarity, they cannot help us identify or quantify the specific declines that followed specific land-use changes.

Fishing catch records provide quantitative data about change over time, but they too have problems.³² Fish hauls reflect effort and technology, not just the number of fish swimming in the lake. The catch data show relatively low catches of lake trout and whitefish between 1872 and 1893, which tells us less about the populations of fish than about the size of the fishing industry. Catch per unit effort is a more useful measure, because it adjusts for the number of fishermen and the efficiency of their gear, but it still offers only an estimate of the fish that swim under the surface. Fishermen, like travellers, may lie about catches for reasons of their own. Nevertheless, we can use available data to get a sense of changes in fishing effort and

production over time and, from that, a proxy estimate of changes in fish populations.³³

In Lake Superior, 4.4 million pounds of lake trout were caught in 1885; this amount had risen to 5.8 million pounds by 1899.³⁴ In 1880, \$1.5 million was invested in Great Lakes fishing, while a decade later, \$5.9 million was invested. But the ratio between capital invested and returned plummeted, suggesting that fish populations were being depleted. In 1880, for every dollar of capital invested, the harvest yielded \$1.23; by 1890, the return had dropped to \$0.46.³⁵ The key point from these records is that, while we do not know much about the pre-commercial fishing populations of lake trout in Lake Superior, we do know that well before sea lamprey were noticed in Lake Superior, intensive fishing combined with habitat loss and pollution had already led to a drop in lake trout populations.

Does this matter? As Ray Hilborn and Ulrike Hilborn argue in *Overfishing*, population declines are an unavoidable function of fisheries.³⁶ But lower populations can still be sustainable over a long time, provided that harvests are not greater than recruitment (i.e., the number of young fish that make it to a certain age, usually the age at which a fish can be harvested). So, were lean and siscowet lake trout populations sustainable under the fishing pressures they experienced? They might have been, had additional ecological stressors—invading lamprey, habitat loss, sedimentation, toxic pollution—not also come into play as factors. But unpredictable ecological stressors are always part of complex systems. Historically, fisheries managers have tried to calculate the maximum sustainable yield, or the highest possible rate of fishing that a population can withstand. But, as modern fisheries biologists are increasingly arguing, under fluctuating environmental conditions and multiple stressors, it is risky to maximize fish harvests. What seems to work when environmental conditions are stable can make populations vulnerable to collapse when a new stressor (such as lamprey) enters the picture.³⁷

As fishing pressures, habitat loss, and pollution increased throughout the Great Lakes, people noted the collapse of one fish population after another. By the 1870s, native fish communities in much of Michigan, for example, were in sharp decline, from a combination of overharvest, pollution, dams, and habitat destruction. Unable to implement harvest regulations, the state responded by creating hatcheries, hoping that culturing and stocking large numbers of fry (young fish) would solve the larger ecological

problems. For reasons that historian Joseph Taylor enumerates in *Making Salmon*, this did not work. Margaret Bogue's study, *Fishing the Great Lakes*, explores in great detail the political responses to overfishing in the Great Lakes. Bogue shows how wholesale fish dealers such as A. Booth and Company quickly monopolized the industry. Fishermen squeezed by declining harvests and predatory pricing used ever more intense technologies to catch ever declining fish. Governments tended to blame the fishermen for dwindling fish populations, while fishermen tended to blame habitat destruction. When governments did try to respond to clear signs that fish populations were collapsing, their measures were ineffective because jurisdictions were fragmented across two nations, several tribes, three states, and one province.

Sea Lamprey

When the sea lamprey came, the lake trout went away. Or at least that is what the data on Wisconsin and Michigan commercial trout fishing suggest. But of course the story is more complicated.

Sea lampreys attach to lake trout near their hearts and suck their bodily fluids. Adult siscowet, which can survive parasitism at higher rates than can the lean lake trout, may have gaping, oozing wounds from numerous lampreys.

Where did these lamprey come from? Sea lamprey had been recorded in Lake Ontario by the 1830s. Many biologists believe that sea lamprey found in Lake Ontario represent relict populations from the last Pleistocene glaciation. Analysis of mitochondrial DNA supports the hypothesis that sea lamprey are native to Lake Ontario.³⁸ However, it was not until the 1890s that sea lamprey in that lake threatened commercial fish populations.³⁹ In 1894, investigators reported that lamprey were often found on Lake Ontario whitefish—and that these were not native freshwater lamprey typically found in creeks. Waldman and colleagues argue that sea lamprey populations in Lake Ontario may have remained rare because of cold temperatures and lack of good habitat for ammocoetes, that is, silty bottoms. Deforestation, industrial development, and pollution that followed the opening of the Welland Canal led to warming water temperatures and silty streams: favourable conditions for sea lamprey populations to expand.⁴⁰

Niagara Falls had once blocked the movements of fish from Lake Ontario into Lake Erie and from there into the upper Great Lakes. When modifications to the Welland Canal were completed in 1919, ocean fish (including sea lamprey) could more easily migrate up into the upper Great Lakes when searching for new tributary streams for spawning. Over the next twenty-five years, sea lamprey moved into Lake Superior, using its many tributary streams for spawning and juvenile habitat.⁴¹ When sea lamprey began to devastate Lake Superior lake trout, the Welland Canal was a convenient target for blame.⁴²

Yet this story is too simple. Decades before the 1919 Welland Canal modifications that allowed free passage of oceanic fish into the upper Great Lakes, biologists were already noticing that some lamprey were not only present but also already attacking fish. Yet lamprey populations remained low. For example, the biologist Samuel Wilmot noted in 1893 that lamprey in Lake Huron and Georgian Bay were attacking whitefish and other fish. In 1915—still four years before the canal modifications—the zoologist B.A. Bensley described two different species of lamprey in Georgian Bay: one freshwater species, long known as native to the upper Great Lakes, and another new species similar to what is now known as the sea lamprey. Bensley called this new species the “lake lamprey” and described it as a “dwarfed fresh water representative of the marine lamprey.”⁴³ These records suggest that the Welland Canal modifications alone do not explain why sea lamprey suddenly became a problem.

Sea lamprey populations quickly exploded in Lake Superior—not just because the Welland Canal allowed their passage, but because habitat changes due to logging, farming, and mining created favourable habitat. To understand this, we need to understand a little bit about sea lamprey development and a little bit about habitat changes in the watershed. Sea lamprey require three distinct but interconnected habitats. Spawning adults need clear brooks with fast water and sand or gravel bottoms. These brooks must be connected by free-flowing streams to larval habitat, which typically consist of slow-moving water in medium to large streams, where the larvae spend up to six years buried in soft silt and sediments. During development, they require silty conditions—conditions that were once fairly rare in most Lake Superior tributaries, but that became much more prevalent after deforestation and farming caused massive erosion.⁴⁴

Increased water temperatures caused in part by deforestation also led to increased lamprey hatching and growth rates.⁴⁵

Lamprey, in other words, cannot mature in cold, clear waters, but they thrive in slow, sediment-laden streams—habitats that were once rare in the Lake Superior watershed. But a century of logging, mining, and farming had turned many of the lake's once clear and cold tributaries into silty, warmer, shallower streams, making them excellent lamprey habitat. Lamprey triggered a sudden threshold change. Like the proverbial straw that broke the camel's back, they were not the sole cause of lake trout crashes, but they were the final stressor that pushed the populations over the edge of a cliff.⁴⁶

Lake Trout Recovery

Serious attempts to control sea lamprey began in 1950, with the installation of mechanical barriers that blocked spawning runs. Electrical barriers across 132 Great Lakes tributaries had been installed by 1960. However, these barrier control measures were not perfect, and enough sea lamprey snuck through them to continue hammering the lake trout.

In 1958, a chemical lampricide (and potent endocrine disruptor) named 3-trifluoromethyl-4-nitrophenol (TFM) was developed that killed larval lamprey in streams without killing adult trout. That is, at the concentrations needed to kill lamprey, TFM did not kill lake trout, but the chemical did kill many stream invertebrates that were essential for maintaining the health of fish populations. In an attempt to control lamprey ammocoetes without devastating macroinvertebrates, fisheries biologists developed treatment protocols that called for tributary streams to be poisoned every three to five years, giving the invertebrates some time to recover before the lamprey recovered.

In the 1970s, sea lamprey populations in treated areas were found to be severely skewed in sex ratio, with few males. In the 1990s, researchers discovered that TFM was an estrogen agonist that affected male lamprey development. Few studies have been done on its hormonal effects on other species, so we simply do not know how treatment of tributary streams might or might not be contributing to the continued decline of the endangered coaster trout and other fish that require tributary habitat. There is no

question but that chemical control was necessary for lake trout recovery. Yet chemical control alone was not sufficient. A combination of hatcheries, barriers, habitat restoration, toxic-waste reductions, and fishing restrictions were important factors in the recovery.⁴⁷

Even with coordinated recovery efforts focusing on sea lamprey control, breeding populations of lake trout have not been restored to any of the Great Lakes other than Lake Superior. Contamination from out-of-basin sources may partly explain this failure to breed. Recent research has established a connection between dioxin levels, larvae mortality, and lake trout decline in Lake Ontario. Dioxins are byproducts of industrial processes; they typically form during the burning of chlorine-containing waste products or during herbicide production.⁴⁸

Lake trout are extremely sensitive to early-life-stage mortality associated with dioxin exposure.⁴⁹ At 30 parts per trillion (ppt), dioxin will begin to kill some lake trout larvae. At 100 ppt, no lake trout larvae survive. Measurable levels of dioxins first showed up in Lake Ontario in the 1930s, and between 1950 and 1975, levels were above 100 ppt. This meant 100 percent mortality of larvae. Only hatchery fish could survive in the lake, and they did not survive for long.⁵⁰ In Lake Superior, dioxin levels never reached those found in Lake Ontario, which may be part of the reason why breeding lake trout populations did manage to survive.⁵¹

Dioxins are not the only contaminants that affect lake trout. In the early 1980s, biologists discovered that Lake Superior lake trout were contaminated with high levels of the detritus of industrial civilization, including PCBs, DDT and its metabolites, toxaphene, and dioxins. Pollution had not been diluted into the deep lake, but instead had become concentrated in the fish that people were eating. Grassroots fury at governments and corporations eventually led to a set of regulatory reforms that banned or strictly limited persistent organic pollutants, and a gratifyingly rapid response was seen in the levels of contaminants measured in fish tissue. Those contamination levels, however, soon levelled off well above zero, even decades after bans were instituted. For example, phenolic compounds from resins, dyes, pulp mills, and petrochemical plants continue to be ubiquitous pollutants in lakes and rivers (TFM, the lampricide, is a phenolic compound as well). Fish exposed to phenols may show changes in thyroid and sex hormones, leading to growth and sexual maturation problems as well as immune

system changes. But no studies have yet assessed the impacts these common pollutants may have had on entire populations.⁵²

Because siscowet have such high fat levels, they tend to accumulate higher levels of many toxic compounds than other fish, and these compounds can suppress growth and reproduction of individual fish. Ironically, the toxic chemicals also suppressed commercial fishing, which may have given the siscowet additional respite from human pressures. In Wisconsin, siscowet thrived in the St. Louis River estuary (near Duluth and Superior) where, from the 1910s on, pulp mills and oil refineries released wastes that accumulated in siscowet fat and gave the fish a bad taste. Freed from fishing pressure, these populations thrived even in the face of sea lamprey invasions, when the lean lake trout that were being heavily fished collapsed. Similarly, decades later, in the 1980s, Canada banned the sale of siscowet when they were found to be high in PCBs.⁵³ Even with continued sea lamprey predation, siscowet stocks began to recover while those of the lean lake trout continued to decline, suggesting that fishing had been a significant factor in the population crash.

Siscowet lake trout were the fish upon which the first commercial fishery in Lake Superior was built. Yet they survived environmental change better than the other varieties, for reasons that are not yet entirely clear.⁵⁴ Their use of the greatest depths in Lake Superior made them less vulnerable to harvest pressures. Additionally, they rarely spawn in the nearshore habitats, so they are less affected by habitat loss and pollution during their most vulnerable life stages. When they do survive lamprey parasitism, siscowet and lean lake trout have different responses (called sub-lethal responses): siscowet mount an immune response, which drains their lipid reserves but allows them to combat parasitism; lean lake trout are more likely to show an overt stress response. Siscowet show higher lamprey wounding rates than do leans, possibly because leans are more likely to die from parasitism; siscowet are more likely to survive, yet with reduced fecundity and growth.⁵⁵

Climate Change and Lake Superior

Climate change is adding an additional set of stressors to Lake Superior's ecosystems. Since 1980, Lake Superior's water temperatures have been

warming at twice the rate of increases in air temperature. Ice cover is diminishing significantly; total ice cover on the lake has shrunk by about 20 percent over the past thirty-seven years.⁵⁶ Decreased ice cover affects lake trout habitat and reproduction. For example, many salmonids have higher reproductive success under ice cover, so reduced ice cover may be leading to changing fish populations. Decreased ice cover also leads to greater evaporation, which in turn lowers water levels.

Total precipitation in the Lake Superior basin may not change over the next century, but models predict that summers may be drier and hotter, while spring storms may intensify. By 2100, summer temperatures there may resemble current summer temperatures in central Kansas, 1,440 kilometres (896 miles) south. More intense early-season rains could increase runoff in the spring and lower water in the summer, while also increasing sediment and nutrient loads in tributaries and the nearshore environment.

What does this mean for lake trout? Not surprisingly, it could be bad news for the fish. Increased water temperatures and increased runoff in Lake Superior may tip the lake over from being an oligotrophic lake with abundant oxygen in the hypolimnion to becoming a more nutrient-rich lake. More nutrients might sound like a good thing for many fish, but this is not necessarily true for lake trout. Lake trout, as discussed above, have thrived in Lake Superior because the depths—the hypolimnion—remain rich in oxygen even in the hottest months of the summer. These depths offer lake trout critical refugia from predation and fishing pressure, and they are probably a significant element in lake trout's historic resiliency to environmental change. But if air temperatures continue to warm and water temperatures continue to increase at twice the rate of air temperatures, algal blooms are likely to increase and the lower levels of the lake will become depleted of oxygen, thus triggering a dramatic loss of habitat for lake trout.

While lake trout do not thrive in warming temperatures, sea lamprey do. When water temperatures warm, sea lamprey feed faster, develop into adults more quickly, and lay more eggs. Other invasive species, such as zebra mussels, also like the warming temperatures; further, they can move toxics that were bound to sediments back up into the water column and, from there, into fish.

Climate change and endocrine-disrupting chemicals may magnify each other's effects. Researchers in Australia found that sub-lethal

concentrations of two pesticides can significantly reduce the tolerance of some freshwater fish to increasing water temperatures—a finding with disturbing implications for lake trout and other cold-water fish.⁵⁷

Conclusion

Why does it matter to historians why one fish in one lake nearly vanished? Environmental history is filled with similar stories. The important thing about lake trout is that they were resilient for so long—until suddenly they were not. They managed to persist through deforestation and its associated siltation, through intensive commercial fishing harvests and unrestricted pollution. Moreover, people in the basin had plenty of warning that this last great fishery might collapse if fishing restrictions were not implemented and enforced. Lake Superior lies at the top of a Great Lakes Basin filled with examples of fisheries that had already collapsed in lakes that had become too polluted to support much aquatic life.

Yet, as Bogue shows, the political chaos of different jurisdictions meant that few effective actions were taken to regulate the catch, protect spawning habitat, or clean up the nearshore environment.⁵⁸ On the land, the chaos of local, state, federal, and provincial laws and policies may have benefitted forests, for it probably shaped an increased ecological diversity in the recovered forests. But in the water, that political fragmentation had very different effects, leading to a regulatory paralysis that thwarted effective action to prevent the collapse of the lake's fisheries.

Into this context swam the sea lamprey, an easy target for blame. But the lamprey never entirely explained the collapse of lake trout. First, the timing was off. Lamprey had been in Lake Ontario long before lake trout populations began to drop, and the lamprey arriving in Lake Erie initially had little effect on lake trout. Similarly, commercial fishing pressures alone do not explain the collapse, because other fish that crashed at the same time were not being commercially fished. For example, populations of four-horned sculpin and burbot also declined sharply, and they are generally not netted by commercial fishermen. Finally, efforts to remove sea lamprey and reduce overfishing did not lead to recovery of breeding populations, except in Lake Superior. Hatcheries still stock all the lake trout that swim in the other Great Lakes, where they are either quickly

caught by fishermen or sucked dry by the sea lampreys that have escaped chemical control.

Why then have biologists and agencies placed so much emphasis on lamprey? Perhaps because it has proven to be much easier to coordinate lamprey control efforts across political boundaries than to coordinate regulations on fishing effort or gear. Sea lamprey were an easy scapegoat, but as Taylor argues, “there has also been an evolving awareness in fisheries management over the last half century of the dynamic relationship between fish and habitat, and the conception of relevant habitat has expanded to include much greater sensitivity to chemicals and whole watershed factors. The most obvious example of this evolving awareness is the increased concern for non-point-source pollution, something that simply was not in the lexicon before the 1980s or 1990s.”⁵⁹

One key lesson of this history is that, while terrestrial and aquatic ecosystems are interconnected in Lake Superior’s watershed, their management is rarely integrated. Events within the basin helped to destroy the lake trout, but processes originating far outside the basin had perhaps even more of an impact. Yes, pulp mills dumped toxic waste over spawning grounds, but the pollutants that blew in from coal plants and industrial agriculture thousands of miles away may have had greater effects on fish. Local fishermen took too many fish, but market domination by A. Booth and Company continued excessive fishing harvests even after fish populations had begun to dwindle. Local towns never managed to control dumping, and slicing up the basin into multiple jurisdictions, each with different political priorities, made effective regulations elusive. Lake trout populations, resilient as they had been for decades, eventually crashed because of multiple stressors at multiple scales. Lamprey may have pushed the fish over the cliff, but land-use change, pollutants, and overfishing had already dragged them right to the edge.

Notes

- 1 Thanks to the Bad River Band of Lake Superior Tribe of Chippewa Indians and to my colleagues on the Lake Superior Binational Forum for their generous insights. Thanks also to Lynne Hearsley and Daniel Macfarlane for fostering this project and to the other authors who participated in a stimulating workshop during the summer of 2012.

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- 42 Bogue reports that "in 1921, a fisherman caught and brought into the Royal Ontario Museum in Toronto an 'eel,' the like of which he had never seen in Lake Erie. Biologists identified it as a sea lamprey like those found for many decades in Lake Ontario, where in the 1920s it was on the increase." *Fishing the Great Lakes*, 330.
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