

Effects of Winter Hypoxia on Fish Communities in Northern

Wisconsin

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Chapter 1

The ecology of fish under the ice and the effects of winter hypoxia on lake
fish communities

Winter Fish Ecology

Freshwater fish are a critical component of North America's aquatic ecosystems. They act as primary, secondary, and tertiary consumers, and interact with a wide variety of invertebrate and plant life. They are often involved in trophic cascades that alter the ecological characteristics and water quality of lakes. Fish are also an important economic resource worldwide, with millions of people yearly participating in angling, commercial fishing, and related activities. There are numerous studies of fish during the ice-free season examining their diet, predator evasion, prey location, mating, and schooling activity. However, much less is known about the ecology of fish in under-ice conditions, especially their resource use in the northern tier of North America (Hampton et al. 2017). While some studies on the topic exist, many focus on European fish assemblages or other aspects of fish ecology during the winter.

Winter is generally a time of low resource availability and high stress for fish. (Johnson and Evans 1996). Light availability is reduced due to decreased day length, low sun angle, and absorption and reflection of light by ice and snow. Light attenuation can be high for snow-covered ice, with only about 2-10% of the available light reaching the water (Shchapov et al. 2021). This decrease in light makes the euphotic zone significantly smaller and the rate of primary productivity of the lake lower, thereby decreasing the amount of phytoplankton and zooplankton present (Hampton et al. 2017). The low productivity limits food availability during the winter for many aquatic life forms, including algae, plants, zooplankton, insect larvae, and fish. During the winter, temperatures range from 0 to 4°C in ice-covered lakes, slowing the metabolism of plants and animals in this period. Although the slowed metabolism of fish may reduce the

amount of food they need, it may not be enough to offset limited food availability. Some fish may not move as quickly or catch prey as efficiently during the winter, limiting their ability to obtain food (Johnson and Evans 1996, Malinovskyi et al. 2020).

Activity Levels and Diet

Fish species exhibit varying amounts of activity and foraging during the winter. For example, brown bullheads (*Ameiurus nebulosus*) did not eat at all in a 2° C Connecticut pond, while brown bullheads in a warmer, heated waterbody nearby ate a variety of food during the same period (Massengill 1973). Rainbow smelt (*Osmerus mordax*) in Lake Michigan had fewer stomach contents in winter than in summer and fed less during the winter (Foltz and Norden 1977). Largemouth bass (*Micropterus salmoides*) in Wisconsin and Michigan had few prey items during the winter, while yellow perch in the same lakes were active predators throughout the entire season (Sullivan 1986). Furthermore, despite their warm water preferences, pumpkinseed (*Lepomis gibbosus*) in Canada readily fed in cold conditions, and 88% of the fish collected in the field during the winter had food in their stomachs (Rooke and Fox 2020). Few fish in Lake Opinicon, Ontario fed in the winter except for yellow perch (Keast 1978). Bluegill in winter in Michigan and Ontario ate far fewer prey items in winter compared to summer, although there were food items encountered in the majority of fish examined (Moffet and Burton 1943, Keast 1978, Rooke and Fox 2020). Yellow perch ate much more than bluegill during the winter, evidenced by their larger and fuller stomachs (Moffet and Burton 1943). In a study on Fish Lake and Little Cataraqui Creek, Ontario, six species of fish (mostly Cyprinid species) varied widely in their feeding habits, with between 25% and 75% of fish from each species having food in their stomachs during

winter (Keast 1968). Smaller fish observed by Keast (1968) had higher relative rations than larger fish. The absence of food items in some fish stomachs could have been either due to a lack of suitable prey or low activity preventing the fish from catching the prey (Keast 1968). There may also be sex-specific differences: female fish need to eat more than male fish in some species, as many fish develop gonads during the winter period in preparation for the spring spawn (Foltz and Norden 1977, Henderson et al. 2000, Malinovskyi et al. 2020).

Fish eat a variety of food items in winter, with shifts in prey occurring between the ice-free growing season and winter. Yellow perch in Wisconsin ate many *Daphnia* during the winter, although the *Chaoborus* that were also eaten were larger in size and likely contributed significantly to energy input (Hasler 1945). Yellow perch in Michigan ate juvenile bluegill, large numbers of zooplankton like *Ostrococha* and *Daphnia*, and insect larvae (Moffet and Burton 1943). Insect larvae (mainly mayflies) made up the majority of stomach volume in early winter for small perch (<120 mm), while later in the winter zooplankton were more common. Medium-sized yellow perch (120-139 mm) ate around 2/3 fish by volume and 1/3 invertebrates by volume, while larger perch (>140 mm) ate mostly fish. In this case, the fish they consumed were mostly small bluegill (Moffet and Burton 1943). There were no Trichoptera (caddisflies) found in six species of fish in Ontario, and “cladocera and ostracoda occurred in all fish, chironomid larvae and Copepoda in about two thirds, and Amphipoda, Ephemeroptera nymphs, and molluscs in about half” (Keast 1968). Copepods and isopods were found in winter fish diets, but not in summer diets. Some of the fish had as diverse a diet in summer as in winter, while others had a much less diverse diet, with some species only having one

third of the diversity of their summer diets (Keast 1968). Bullhead (genus *Ameiurus*) in Canada ate a wide variety of food in winter, including fish, zooplankton, worms, and molluscs in their diet (Massengill 1973). Fish contributed most to the diets of the bullhead.

Energy, Growth, and Osmoregulation

Winter conditions can cause a number of external stressors for fish.

Osmoregulation can be an important stressor, and has been shown to be more of a factor in death than starvation in very cold waters (Johnson and Evans 1996, Bernard and Fox 1997, Curry et al. 2005). Cold temperatures make osmoregulation more difficult because of changes associated with ion transport channels and membrane permeability. If very cold temperatures are experienced for long enough, fish cannot regulate the balance of necessary chemicals in their body, leading to decreased survival. Smaller fish appear to have increased osmoregulatory failure and require more energy per unit of mass to maintain osmoregulation, reducing their food reserves (Johnson and Evans 1996).

Fish can lose energy reserves due to starvation, osmoregulatory stress, or reproductive allotment during the winter months. Walleye were found to have lower caloric content in the spring than in the fall (Kelso 1973). Lipid content decreased for common roach (*Rutilus rutilus*, a European species) in a eutrophic lake but increased in a large (and presumably less eutrophic) lake (Kirjasniemi and Valtonen 1997). Smallmouth bass (*Micropterus dolomieu*) subsist on accumulated energy reserves over winter (Shuter et al. 1980), and individuals in one lake lost 22-54% of their reserves during the winter (Curry et al. 2005). Rainbow smelt had less caloric density in May than in October, indicating a loss of energy reserves (Foltz and Norden 1977). Yellow perch in Lake

Michigan lost caloric density from the fall to the winter (Roswell et al. 2014). Yellow perch in Lake Erie also lost caloric density through the winter, measured through calorimeters and lipid content; ovary production in females increased the loss in energy compared to males (Henderson et al. 2000). In contrast, yellow perch in another lake retained energy during the winter (seen through lipid amounts), while largemouth bass lost energy (Sullivan 1986). An additional factor in increased energy loss is gonad development; many fish develop gonads during the winter for spring spawning, increasing energy needs during the winter (Foltz and Norden 1977).

Lipids act as an energy storage medium in many species of fish, and variations in the amount of lipids present can help describe energy losses and gains during the year (Sullivan 1986, Fernandes and McMeans 2019). Several studies on yellow perch have found lipid content to decrease during the winter (Henderson et al. 2000, Roswell et al. 2014). In contrast, another study found that yellow perch, a cool-water adapted species, had consistent lipid content throughout the winter, while largemouth bass, a warm-water adapted species, exhibited a significant loss of lipids (Sullivan 1986). A literature review on winter lipid variations in multiple fish species found no significant difference between warm, cool, and coldwater species (Fernandes and McMeans 2019). Although the variously adapted species may differ in their activity levels during the winter, other factors played into lipid variation, such as incorporation of lipids into gonad tissue and spawning times (Fernandes and McMeans 2019).

Fish of various species could potentially grow in mass and length during winter if the appropriate food intake is available. However, due to the limits of prey production in the winter, some species may not have the resources to exhibit positive growth. Brown

trout (*Salmo trutta*) and arctic charr (*Salvelinus alpinus*) raised in semi-natural conditions failed to show any positive growth rates (measured by mass), while fish in laboratory conditions exhibited some positive growth depending on light level (Heiland et al. 2011). Brown trout in a stream environment grew in length and mass during the winter and ice cover was positively correlated with growth rates (Watz et al. 2016). Atlantic salmon (*Salmo salar*) exhibited negative growth rates when raised in semi-natural conditions in Norway, while those in more controlled laboratory settings had both positive and negative growth rates (Finstad et al. 2004). Yellow perch had a positive growth rate in Lake Michigan and Lake Huron during winter with fish in Lake Michigan gaining 0.1-1mm of length per day (Fitzgerald et al. 2004, Diana and Salz 1990).

Mortality

Starvation of fish can occur during the low productivity conditions of winter if low daily rations are experienced. Age-0 fish (fish hatched during the previous summer) are particularly prone to overwinter starvation, as they are less able to build up food reserves due to their small size (Johnson and Evans 1996, Kirjasniemi and Valtonen 1997). Not only are Age-0 fish less able to build up lipid reserves, but they lose more energy per unit body mass over time than larger fish due to comparatively high metabolic rates (Bernard and Fox 1997, Kirjasniemi and Valtonen 1997). As food is usually very limited in winter, up to 50% of young and small fish die in some lakes due to starvation (Kirjasniemi and Valtonen 1997).

Increased Age-0 mortality during the winter relative to summer months has been documented in a variety of freshwater fish, including white perch (*Morone americana*), smallmouth bass, yellow perch, largemouth bass, and common roach (McLean 1981, Post

and Evans 1989, Miranda and Hubbard 1994, Johnson and Evans 1996, Kirjasniemi and Valtonen 1997, Shuter et al. 2012). The minimum size where mortality increases depends on the species and particular population, with lake conditions, temperature, amount of eutrophication, and other factors also influencing mortality rates (Bernard and Fox 1997, Kirjasniemi and Valtonen 1997, Curry et al. 2005). Yellow perch, for example, are predicted to have a minimum survival length of about 57 mm in some temperate lakes (Post and Evans 1989, Fitzgerald et al. 2004). Yellow perch in Lake Michigan reached an average size greater than that minimum survival length, and experienced low winter mortality over many years; mortality may have been higher if the fish did not grow to the observed size (Fitzgerald et al. 2004). Another study on Lake Michigan found evidence for increased mortality for small fish, due to increased rates of energy depletion (Roswell et al. 2014). Adults of many species face similar struggles with increased mortality during the winter, but at lesser rates than small Age-0 fish. Based on these factors, understanding the amount of food fish consume, as well as the relative nutritional value of different food categories, is important in determining whether a fish will have enough energy to survive the winter.

Fish species may exhibit differing mortality rates depending on the pH and oxygen levels of a lake during the winter. One study found that bog lakes severely limited species distributions, partially due to oxygen-poor water (Rahel 1984). Oligotrophic, oxygen-rich lakes contained many centrarchid (sunfish) species, while bog lakes only contained yellow perch and mudminnows (Rahel 1984). Condition tolerances during the winter limit what lakes certain species can inhabit.

Overwinter Lake Hypoxia

One major cause of overwinter fish mortality in some lakes is hypoxia, or the absence of sufficient oxygen in a lake for fish to respire and maintain homeostasis (Greenbank 1945, Ultsch 1989). In northern-temperate lakes, hypoxia can occur during all seasons of the year, but one of the most common and critical times of hypoxia is during winter (Greenbank 1945). Several factors lead to the depletion and possible complete removal of oxygen from much of a given lake. During the summer, mixing of the water-air interface by wind replenishes oxygen used up through respiration by a variety of organisms. However, during winter in northern temperate lakes, ice forms, creating a barrier and preventing the mixing of air and water by wind action. In cold climates, ice can remain on lakes for several months. The ice effectively blocks oxygen from diffusing into the water, unless there are large enough cracks to penetrate through the ice and allow gas diffusion to occur (Greenbank 1945, Matthias and Barica 1980). The oxygen present in late fall becomes isolated when the lake freezes, creating a limited supply of the gas that often diminishes as the season progresses unless produced by phytoplankton or aquatic plants under the ice (Meding and Jackson 1980). Lakes in northern-temperate areas, except for extremely eutrophic ones, are fairly well oxygenated at ice formation, as fall mixing brings oxygen into a homogenous and cold (approximately 4 °C) water column that can hold large amounts of the gas. However, fish, invertebrates, and bacteria consume the oxygen as winter progresses (Matthias and Barica 1980, Brabin and Pepas 1983). By mid to late winter, conditions in much of a lake can become completely anoxic, leading to fatal conditions for most species of fish,

particularly if aquatic plants and phytoplankton respire as much oxygen as they produce (Rahel 1984).

Various factors in a lake can mitigate or enhance the severity of hypoxia during the winter. Colder winter seasons with longer periods of ice cover and deeper snow tend to have more hypoxia and subsequent winterkills, as the water-air interface is blocked for an increased duration, leading to longer periods of isolated oxygen and limited light penetration due to snow and ice cover (Fang and Stefan 2000). Depletion of oxygen by organisms occurs for a longer time under these extended ice-on conditions.

Photosynthesis under the ice by phytoplankton, on the other hand, acts as a mechanism to maintain or even increase oxygen levels during the winter (Cooper and Washburn 1949, Barica et al. 1983). The rate of photosynthesis, and thus the amount of oxygen produced, depends on the amount of light available in a lake. Snow, ice, and lake depth are the main determining factors on how much light the phytoplankton can receive. In general, light levels under the ice are much lower than in summer due to absorption and refraction by snow and ice, leaving only the top portion of the lake (generally the first meter or two) sufficient light for photosynthesis (Greenbank 1945, Cooper and Washburn 1949).

Thicker ice, deeper snow, and more opaque ice all result in lower amounts of light reaching the top layer of the lake. Years with high snowfall are especially prone to winterkill, as even a small layer of snow can block most if not all of the light reaching the water (Cooper and Washburn 1949, Barica et al. 1983). If the light reaching the top of the water is sufficient for photosynthesis to occur (in years with thinner, clearer ice and less snow), oxygen can remain at sufficient levels for fish to utilize at the ice-water interface (Davis et al. 2020). Many species of fish use this top layer as a refuge in years when

oxygen content elsewhere is low or zero (Lewis 1970, Davis 1975, Gee et al. 1978, Knights et al. 2011). Inputs by open-water streams and groundwater can increase the oxygen present at certain parts of a lake (Greenbank 1945, Magnuson and Tonn 1982, Rahel 1984). Fish species that cannot tolerate low-oxygen conditions often travel to lake inlets or even swim up streams connecting lakes to survive hypoxia. In spring, when oxygen levels rise, the fish swim back into the lake.

In general, shallow and eutrophic lakes have the highest rates of winterkill. Winter fish kills are well documented in shallow lakes: the lakes have a higher surface-to-volume ratio, providing more surface area for bacteria in the substrate to decompose organic matter and consume oxygen (Mathias and Barica 1980, Meding and Jackson 1980, Rahel 1982, Barica et al. 1983, Tonn et al. 1990, Clilverd et al. 2009, Balayla et al. 2010, Shuter et al. 2012). Consumption of organic matter (mainly by bacteria as well as other microorganisms) is the primary path for oxygen depletion in lakes during the winter; fish and zooplankton also consume oxygen, but their contribution to lake-wide respiration is minimal in comparison (Greenbank 1945, Mathias and Barica 1980). Shallow lakes also have a shorter water column than deep lakes, providing a smaller reservoir for oxygen. Eutrophic status also puts a lake at high risk of hypoxia in the winter (Mathias and Barica 1980, Babin and Prepas 1983, Danylchuk and Tonn 2003). Eutrophic lakes build up more organic matter than oligotrophic lakes, mainly during the summer when production rates are higher; this organic matter provides a large supply of material for bacteria to consume during the winter months. That high consumption increases oxygen usage, quickly depleting a eutrophic lake's oxygen supply (Meding and Jackson 1980). Areas with high organic input from the surrounding watershed also have

the potential for higher rates of winterkill, as the input increases organic matter in a manner similar to primary productivity. Lakes further along a gradient in succession (from deep and oligotrophic to bog e.g. Lindeman 1942) are especially vulnerable, as they tend to be shallower and have high amounts of organic input from production in the lake and in the surrounding watershed (Rahel 1984).

For years, managers of lakes have attempted to mitigate the hazards of winterkills to preserve sport fish populations and fish communities in general. These methods either directly (through aeration or creating spaces for diffusion from the atmosphere) or indirectly (through increased photosynthesis) attempt to add oxygen to a lake. Aeration provides perhaps the best method of increasing oxygen, accomplished by bubbling gas directly into the lake and maintaining areas of open water for direct diffusion. This method prevents winterkill (as well as summer hypoxia) in a number of lakes if properly applied (Greenbank 1945, Stefan 1989). This method has been used successfully in many lakes to help prevent winterkill (Fast 1994). However, it can be quite expensive to maintain. Chopping holes in the ice to allow gas to diffuse from the atmosphere to the water is another possible method (Greenbank 1945), but this requires constant maintenance and the rate of diffusion is fairly slow in small openings. Removing snow provides oxygen indirectly by increasing the amount of light and thus the amount of photosynthesis that phytoplankton can carry out (Greenbank 1945, Barica et al. 1983). Moving as little as 15% of the snow can produce an appreciable increase in the amount of oxygen present just beneath the ice (Barica et al. 1983). However, this method must be repeated each time the snow falls, increasing the effort required to maintain snow-free ice.

Fish Tolerance and Adaptations to Winter Hypoxia

The lethal implications of hypoxia on fish are extensive. In complete anoxia, all fish species will eventually die, due to the inability to respire or regulate basic bodily functions. When oxygen levels begin to decrease, most fish species will increase their breathing rate, pumping their gills faster to circulate more water and thus more oxygen into their bloodstream (Lewis 1970, Davis et al. 1975, Gee et al. 1978). The exact oxygen concentration at which they will begin breathing faster varies between species. As oxygen levels further decrease, fish movement and coordination deteriorate. Eventually, oxygen delivery to the brain reduces to the point where any coordinated movement is impossible, rendering the fish comatose (Nilsson and Renshaw 2003). Under anoxic winter conditions, in addition to increased breathing rate, fish employ two main strategies to survive. First, many fish species will migrate to the top of the water column to take advantage of increased oxygen concentrations due to photosynthesis (Magnuson et al. 1985, Ultsch 1989, Shuter et al. 2012). The oxygen levels may not be optimal, but they will often be enough to sustain fish when the rest of the lake is anoxic. The exact oxygen conditions at which the fish will move to the top layer again depends on the species, with species that can handle low oxygen levels moving up at a lower oxygen concentration (Gee et al. 1978, Hasler et al 2009). Some Cyprinid species can access microbubbles just under the ice, further enhancing their ability to survive in a low-oxygen environment (Klinger et al. 1982).

The second strategy fish may use to survive hypoxia is migrating to a stream connected to a given lake, either residing by the inlet or outlet or entirely leaving the lake and living in the stream during the winter (Magnuson et al. 1985, Shuter et al. 2012).

Streams usually have higher oxygen concentrations than lakes, and may have direct contact with the water-air interface (being unfrozen), providing fish with oxygen they would not find in an anoxic lake. Fish that migrate out of the lake return when spring arrives (Magnuson et al. 1985, Shuter et al. 2012). Lakes with stream connections can harbor higher species diversity than isolated lakes, as they both provide a high oxygen refuge and act as a corridor for fish to migrate from connected lakes, helping populations to recover faster in a lake experiencing severe winterkill.

Two freshwater fish species, the central mudminnow (*Umbra limi*) and the crucian carp (*Carassius carassius*), have extraordinary adaptations to surviving low-oxygen conditions, enabling them to live in environments inhospitable to most other fish. The central mudminnow, native to central and eastern North America, can directly access air bubbles in the water, enabling them to obtain oxygen when there is little or no oxygen present elsewhere in the water (Magnuson et al. 1983, Klinger et al. 1982). They are sometimes the only species present after an extreme winterkill event. Crucian carp, present in Europe and Asia, have multiple adaptations to surviving low-oxygen conditions as well as complete anoxia. They can increase their gill surface area in a matter of days, allowing them to access scarce oxygen (Nillson and Renshaw 2003). The fish also have an altered hemoglobin that can carry large amounts of oxygen. In complete anoxia, the fish reduce protein synthesis in their organs and reduce brain activity, lowering energy expenditure (Nillson and Renshaw 2003). They can also completely bypass aerobic respiration by relying on large stores of glycogen stored in their liver, allowing them to live for days or even weeks in complete anoxia (Nillson and Renshaw 2003).

Freshwater fish species demonstrate a wide range of tolerances to hypoxia. In general, most fish species are completely healthy in conditions above about 5 or 6 mg/L of oxygen (the most common method of measuring oxygen, along with ppm, a synonym, Davis 1975). Members of the Centrarchidae family, which include species like the largemouth bass (*Micropterus salmoides*), bluegill (*Lepomis macrochirus*), green sunfish (*Lepomis cyanellus*), rock bass (*Ambloplites rupestris*), black crappie (*Pomoxis nigromaculatus*), white crappie (*Pomoxis annularis*), and smallmouth bass (*Micropterus dolomieu*) are generally poor at withstanding low oxygen levels in winter, often being the first to reduce activity or die in a winterkill event (Cooper and Washburn 1949, Petrosky and Magnuson 1973, Hail and Ehlinger 1989, Tonn et al. 1990, Farwell et al. 2007). Largemouth bass and bluegill in particular do not tolerate conditions well below 3 mg/L and 1 mg/L, respectively (Davis 1975). Pumpkinseed (*Lepomis gibbosus*), another member of the Centrarchidae family, fare somewhat better at tolerating low oxygen than bluegill (down to about 0.5 mg/L), even though they are in the same genus (Cooper and Washburn 1949, Farwell et al. 2007). They can potentially live in lakes with moderate winterkill where bluegill do not cope well, reducing the competition they face. Fish of the Salmonidae family, the family of trout and salmon, are not well adapted to low oxygen (Cooper and Washburn 1949, Davis 1975, Gee et al. 1978). Brook trout (*Salvelinus fontinalis*), rainbow trout (*Oncorhynchus mykiss*), and brown trout (*Salmo trutta*) all struggle at conditions below 3 mg/L oxygen (Davis 1975). All of these species generally live in streams or deep, cold lakes, where oxygen concentrations are usually higher than in other lakes during the winter. Some species in the Salmonidae family lack a mechanism to move towards the top of the water in low-oxygen environments,

potentially preventing them from taking advantage of suitable oxygen conditions there in the winter (Gee et al. 1978). Members of the Percidae family vary in their ability to withstand low oxygen. Walleye (*Sander vitreus*) are similar in tolerance to the centrarchids, dying earlier than other fish species and generally tolerating conditions above 2.0 mg/L (Davis 1975). Yellow perch (*Perca flavescans*) are well adapted to low-oxygen conditions, surviving in places where most centrarchids cannot survive, down to about 0.3 mg/L (Cooper and Washburn 1949). Northern pike (*Esox esox*) and American pickerel (*Esox americanus*), members of the Esociform order, are both tolerant of low oxygen, down to about 0.5 and 0.3 mg/L, respectively (Cooper and Washington 1949, Petrosky and Magnuson 1973). Central mudminnows (*Umbra limi*) are another member of the Esociformes, and as mentioned before, are specialists at surviving extremely low oxygen, enabling them to live where no other species can (Klinger et al. 1982, Magnuson et al. 1983, Tonn and Paszkowski 1986, 2, Shuter et al. 2012). Minnows and carp in the Cyprinidae family are in general tolerant of low oxygen or even anoxia. Fathead minnows (*Pimephales promelas*) have varying tolerances of winterkill, with some sources indicating they die in large numbers during winterkill events, while others document that they can access microbubbles at the top of the water column, providing them with tolerance to low-oxygen lakes as long as primary production still occurs (Klinger et al. 1982, Magnuson et al. 1985, Danylchuk and Tonn 2003, Danylchuk and Tonn 2006). Various other minnow species, like brook stickleback (*Culaea inconstans*), golden shiners (*Notemigonus crysoleucas*), finescale dace (*Chrosomus neogaeus*), northern redbelly dace (*Chrosomus eos*), Iowa darter (*Etheostoma exile*), blacknose shiner (*Notropis heterolepis*), and blackchin shiner (*Notropis heterodon*) survive well in

low oxygen, tolerating conditions of 0.2 mg/L or lower (Cooper and Washburn 1949, Davis 1975, Gee et al. 1978, Magnuson et al. 1985, Rahel 1984). Crucian carp (*Carassius carassius*) can survive in low oxygen and anoxic conditions through their various adaptations (Bronmark et al. 1995, Nilsson and Renshaw 2003). Members of the catfish family (Ictaluridae), specifically yellow bullhead (*Ameiurus natalis*) and black bullhead (*Ameiurus melas*), are also well adapted to low-oxygen concentrations of 0.2 mg/L or less, allowing them to live in areas devoid of more sensitive fish (Cooper and Washington 1949, Rahel 1984).

Winter Hypoxia Effects on Fish Communities

Fish communities can be greatly impacted by hypoxia depending on the tolerances of fish present in a lake. Within a single species, winter hypoxia can alter life histories of fish. Fathead minnows experiencing hypoxia had a lower life expectancy, a faster growth and maturity rate, and a greater allocation of resources into gonad production than in other lakes. (Danylchuk and Tonn 2006). The high mortality due to hypoxia led them to shift to a more rapid life history, focusing on early reproduction. The lower density of fish after each hypoxia event potentially reduced intraspecific competition for the minnows, while at the same time forcing them to focus more on reproduction due to low life expectancy.

Fish communities as a whole can also be shaped by winter hypoxia. The extent to which fish communities are impacted by winterkill greatly depends on the severity of the winterkill, the connections to streams and other nearby lakes, the position of a lake on the watershed, and lake features like habitat complexity and pH (Rahel 1984, Riera et al. 2000). In northern Wisconsin, winterkill has been identified as a major determinant of

fish communities (Tonn and Magnuson 1984). There were two distinct assemblages of fish, one consisting of largemouth bass, bluegill, pumpkinseed, bullhead, and northern pike (the centrarchid-Esox assemblage), and one with mudminnows and other cyprinid minnows (the Umbra-cyprinid assemblage). The centrarchid-Esox assemblages were characterized by either adequate winter oxygen levels or availability of streams that could act as refuges. In lakes that had a lot of oxygen in the winter, largemouth bass were the primary predators, and in lakes with stream connections and lower oxygen, northern pike were the dominant predator. Perhaps northern pike dominated these lakes due to their increased tolerance of low-oxygen conditions over largemouth bass. Smaller fish species consisted of “medium-sized” species with spines that could withstand piscivore predation. The species richness in these lakes was positively correlated with habitat diversity and lake size. Mudminnows and cyprinid minnows were rare or absent as they would easily fall prey to the large piscivores present in the lakes, lacking spines or larger size for defense. Spiny, medium-sized planktivores and insectivores like bluegill, yellow perch, and bullhead were able to evade predation, enabling them to dominate the lower food chain. Additionally, such species are more generalist in diet and can access a wide variety of prey items, enabling them to outcompete mudminnows and cyprinids in foraging. In lakes of this category that had low winter oxygen and stream refuges, many of the fish species were absent in winter, indicating that they moved to the streams for sanctuary. In lakes with inadequate oxygen in the winter and limited stream connections, species like central mudminnow, golden shiner, northern redbelly dace, and pearl dace (*Margariscus nachtriebi*) dominated, with some yellow perch present, making up the Umbra-cyprinid assemblage. Large-bodied fish and species not tolerant of low-oxygen

conditions were not able to survive in these conditions, leaving the more tolerant mudminnows and cyprinids. The tolerant fish species thrived in these conditions, free of predation from large-bodied piscivores. Interestingly, species richness was negatively correlated with oxygen concentration in these lakes. Lower oxygen concentrations potentially reduced fish densities, preventing intense interspecies competition and enabling a wider variety of species to coexist.

Additional studies expanded on the topic by dividing the two species assemblages into three groups by including pH as an independent variable (Rahel 1984). Lakes in northern Wisconsin exist as a gradient from deep lakes with high winter oxygen to shallow, eutrophic, and acidic bogs, with lakes that are pH neutral and oxygen-poor in winter in the middle. This gradient in lakes came from their geological history. Lakes created by glaciation in the Northern Hemisphere generally fill up with organic matter over time due to watershed and lake primary production, building up as a thick layer of sediment that both reduces lake depth and decreases winter oxygen due to bacterial consumption. Eventually, this buildup leads to bogs, which are highly acidic and often devoid of most oxygen in the winter due to bacterial respiration. Lakes vary in position on this gradient depending on initial depth, watershed area, and other factors, leading to differentiation in trophic status, winter oxygen level, and pH. Lakes that have not undergone much succession (e.g. Lindeman 1942) have ample winter oxygen, making them opportune places for centrarchid assemblages, the first category. This species assemblage included species like largemouth bass, bluegill, pumpkinseed, yellow perch, northern pike, rock bass, black crappie, and white sucker (*Catostomus commersonii*). Cyprinid minnows and mudminnows were present in some of these lakes but were not

very abundant due to high predation of their small, spineless body forms and more specialized foraging methods compared to centrarchids. Further along the successional gradient, lakes with low winter oxygen concentrations and neutral pH favored the presence of cyprinid minnows like golden shiner, pearl dace, northern redbelly dace, Iowa darter, blacknose shiner, and fathead minnow. These fish could tolerate low-oxygen conditions, enabling them to thrive in the lakes, free of predation from most piscivores. Central mudminnows were also present in these lakes, although they were not dominant due to competition from the other minnows present in the lake. Furthest along the gradient were bog lakes, characterized by low pH and very low oxygen in winter. In these lakes only two species were present: yellow perch and central mudminnow (except for one lake which also contained golden shiner). These species, comprising the Umbra-Perca group, can tolerate both acidic conditions and low winter oxygen, enabling them to survive where no other species could. Effectively, the first category from earlier research (the centrarchids with high oxygen winters) remained the same, while the second low oxygen category (Umbra-cyprinid) was split into two (cyprinid and Umbra-Perca), based on pH levels (Rahel 1984). Interestingly, lakes with moderately low amounts of oxygen in the winter could support both golden shiner (a species normally abundant only in cyprinid lakes) and centrarchid populations in decent abundance. Lakes that experienced minor winterkill could reduce centrarchids to the point that they would not compete with golden shiners as much, enabling them to survive at lower densities while allowing golden shiners to persist at fair numbers.

Other research compared Wisconsin fish assemblages with similar lakes in Finland to examine if such assemblages were geographically universal (Tonn et al. 1990).

Lakes were categorized into three categories: mudminnow lakes, lakes with low-oxygen winters containing central mudminnow, yellow perch, and some cyprinid minnows; pike lakes, lakes that had low-oxygen winter conditions, stream refuges, and fish communities of centrarchids, yellow perch, and bullheads, with northern pike as the dominant predator; and bass lakes, which had ample oxygen in winter, and centrarchids, yellow perch, and bullheads as the main fish species, with largemouth bass as the main piscivore. While Wisconsin had distinct population categories based on winter oxygen level and other environmental conditions, Finland had more of a gradual gradient of fish communities. Lakes existed on a continuum from more to less species, with no distinct groupings present. There were several reasons for this. Finland has deeper lakes than Wisconsin, reducing the extreme effects found in the bog succession of North America. The lakes in Finland are also more connected than those in Wisconsin, enabling fish to more rapidly repopulate areas disturbed by winterkills or other extreme events. The fish species in Wisconsin are more specialized than the generalists in Finland, perhaps partially as a result of the more specialized and extreme environments present in the area. The generalist fish species survive better in a wide variety of conditions, compared to species like central mudminnow that are abundant only in low-oxygen environments. Even though both Finland and Wisconsin both have glaciated lakes, differences in local topography and environment permit specialization in one location, and generalization in the other. Therefore, even in areas with similar historical geographic events, local effects can have wide-ranging impacts on the specialization of fish communities.

Additional examples help to support the contention that fish communities are shaped by winterkill. Within centrarchid lakes, the extent of bluegill and pumpkinseed

communities could be affected by tolerance to moderate winterkill events. Pumpkinseeds are more tolerant of winterkill than bluegill, having numerous adaptations to living in low-oxygen environments (Farwell et al. 2007). In lakes with ample oxygen, both species coexist; they both share some diet overlap, with pumpkinseed focusing more on mollusks (Mittelbach et al. 1992). However, in lakes with higher likelihoods of winterkill, pumpkinseeds can survive more than bluegill, allowing them to dominate those lakes. In a Michigan lake, two consecutive winterkills eliminated largemouth bass from a lake containing the bass and golden shiner, enabling the golden shiner to become more abundant (Hail and Ehlinger 1989). The golden shiner also became smaller on average, due to the intraspecific competition caused by their abundance.

Extinction and Recovery of Fish Communities in Winterkill Lakes

Extinction events created by severe winterkills over many years can permanently alter fish communities. These extinction events like winterkill can shape fish communities to a greater extent than other factors like lake isolation (Magnuson et al. 1998). Isolation of lakes is also an important factor, as the extent to which a lake is connected to others in a watershed determines the rate at which species repopulate a given lake; however, the possibility of a species disappearing via winterkill is higher than a new or previously existing species traveling from a connected lake. In lakes that are extremely isolated and experience high extinction, species richness is low, containing assemblages like the dual-species Perca-Umbra group, which specialize in low pH, low-oxygen environments (Shuter et al. 2012). Lakes further down in the watershed potentially have a greater chance of recovery from extinction, as surrounding lakes are

more likely to have diverse fish communities that could repopulate lakes affected by winterkill (Kratz et al. 1997).

When winterkill events are not complete, or when lakes have sufficient connection to others to allow for rapid repopulation, recovery of intolerant species can take place. In northern Wisconsin, winterkills in several lakes removed much of the adult yellow perch population, leaving only small perch and central mudminnow (Tonn and Paszkowski 1986). Central mudminnows became much more abundant and overall smaller, as they were no longer preyed upon by the now-dead adult perch, allowing large numbers of juvenile mudminnows to persist. Within a year or two, the remaining small perch reproduced, and some grew to a size larger than 13 cm, at which point they could eat the mudminnows. The mudminnows then decreased in abundance, and the fish community returned to pre-winterkill conditions, with abundant, large yellow perch and sparse amounts of large mudminnows able to evade predation by the yellow perch.

In Finland a shallow lake underwent winterkill, killing many fish present in the lake (Ruuhjarvi et al. 2010). Before the winterkill, it contained pikeperch (*Sander lucioperca*), small cyprinid species like white bream (*Blicca bjoerkna*), common bleak (*Alburnus alburnus*), roach (*Rutilus rutilus*), northern pike, and European perch (*Perca fluviatilis*). The winterkill removed approximately two thirds of the fish in the lake, completely removing some species like pikeperch and severely reducing the number of most other species except for roach. Roach and European perch became abundant in the years following, eating abundant zooplankton and other invertebrates. Pike also increased in number, and the large pike and growing perch ate large numbers of cyprinid minnows, keeping the lake dominated by pike, perch, and roach. Eventually, the growth rate of

perch slowed and piscivory decreased, leading to a gradual return of the cyprinid minnow population in the lake. One reason piscivory declined for European perch specifically was increased fishing pressure: many of the large fish were removed by anglers several years after the winterkill when the lake became a popular destination for angling. This increased the rate at which the small cyprinid minnows were able to recover. Eventually, the lake returned to the state it was before, with all fish species present in normal numbers.

Other Environmental Effects and Trophic Cascades Associated with Winterkill

Winter hypoxia, through trophic cascades, also has the potential to alter other aspects of lakes (Carpenter and Kitchell 1993). If hypoxia removes large piscivores like largemouth bass and northern pike, planktivores can rapidly become more numerous as they are released from intense predation pressure (Hail and Ehlinger 1989, Bronmark and Weisner 1992, Tessier and Woodruff 2002, Jeppesen et al. 2004). The increase in planktivores increases predation on zooplankton and other invertebrates, reducing their population and in turn reducing the population of phytoplankton. A lake influenced in this way has the potential to become less clear as phytoplankton populations increase and shade out macrophytes. When planktivores are removed by hypoxia, on the other hand, opposite effects on the lake can occur (Tonn et al. 2004, Jackson et al. 2007, Balalya et al. 2010). Removal of planktivores reduces predation pressure on zooplankton and other invertebrates, allowing them to increase in density and size (as planktivores usually preferentially prey on larger zooplankton) and eat more of the phytoplankton. The phytoplankton reduce in number, allowing macrophytes to increase in cover and the lake to become clearer. These two opposing cases are not the only results that can come from

hypoxia; in Finland, a lake became clearer after the removal of piscivores, different from the expected effects discussed above (Ruuhijarvi et al. 2010). Planktivores increased in number and reduced the number of zooplankton. However, large amounts of macrophytes present in the lake likely mitigated the amount of phosphorus in the lakes, preventing the increase in phytoplankton that would be expected otherwise.

Synthesis of Winterkill and Fish Communities

Winterkill and its effects on fish communities have a range of variables that may dictate the extent of fish community change (Figure 1-1). The severity of winterkill in a lake can be affected by the frequency of winterkill (every year, occasionally, infrequently), the level of oxygen in the lake during the winter, and the length at which oxygen levels are low enough for fish mortality in a winter. When winterkills happen more frequently, and with low-oxygen or anoxic conditions present for long periods of time in each event, larger impacts on fish community could be expected (Figure 1-1). Fish community change can be measured by species richness (the number of fish species present), a Shannon-Weiner diversity index, a Simpson's index, or a trait-based categorization of the species in a lake. A trait-based category would separate fish into low, medium, and high tolerance fish, allowing for enumeration of species of different hypoxia tolerance. Conditions that could increase the chance of severe winterkills in a lake include a shallow depth, high rates of primary productivity, and long, cold, and snowy winters resulting in a long-lasting, thick layer of ice and snow. Factors that could increase the change in fish community in a lake or the presence of a community of fish highly tolerant of low-oxygen winters include isolation of the lake in the watershed and the absence of high-

oxygen refugia for fish in the winter. Lakes that are isolated from others in a watershed would have lower chances of species recovery through migration, and the absence of high-oxygen refugia like stream connections or photosynthesis in the top layer of the water column would mean that low-oxygen intolerant fish would not be able to find areas to escape hypoxia.

In lakes that are not vulnerable to winterkill, or have winterkill very infrequently, factors like watershed connectivity or stream refugia would not have much impact on the amount of fish community change seen in a lake from winterkills, as these lakes simply do not experience many negative effects from winterkill (Figure 1-1). For lakes with severe winterkill, large impacts on fish community and communities dominated by tolerant fish like yellow perch and central mudminnow would be expected, regardless of other factors (Figure 1-1). Even if species could recover from nearby lakes or find small pockets of refugia from anoxia, the extent of winterkill could be so severe that any intolerant fish entering the lake during winter could perish. In lakes with moderate or somewhat frequent winterkills, factors like connectedness of the lake to the watershed and refugia may matter more, as fish species could easily recolonize the lake in between events or withstand winterkill more readily in refugia (Figure 1-1).

Summary

The winter period clearly has wide-ranging effects on fish communities and lake environments. Reduced temperatures and production can slow fish metabolisms and lead to limits on energy intake during the winter, decreasing fish growth and possibly causing fish to starve if food resources are limited. Mortality of fish during the winter depends on

fish age, species, winter severity, and additional environmental factors, with more severe winters generally having greater consequences for the species inhabiting a winter ecosystem. Hypoxia, one of the primary sources of mortality, affects fish communities extensively and can potentially alter whole lake ecosystems depending on its severity. Winter hypoxia severity depends on season length, ice and snow depth, and photosynthesis in the top layer of the lake. Fish demonstrate varying tolerances and adaptations to hypoxic conditions, and these differences lead to changes in community composition in lakes experiencing a range of hypoxia conditions. The changes brought on by hypoxia can be permanent or temporary, with the recovery of fish communities to prior conditions dependent on the severity of the winterkills, the connectedness of the lake watersheds, and the other environmental conditions present in the ecosystems. If winterkills are persistent, permanent changes can happen in fish communities, with anoxic specialists dominating in lakes experiencing the most severe winterkills. Removal of piscivores, planktivores, or both through winterkill can create top-down trophic cascades in lakes, with effects depending on the species removed. These top-down effects can be mediated by other factors like macrophyte cover, resulting in varying responses of the entire lake environment to a winterkill.

Climate change has the potential to alter winter environments, altering fish community responses to winterkill and other winter conditions. In general, lakes will experience less severe winterkill throughout the world, as warming temperatures in winter reduce the thickness and length of ice presence on lakes in the season (Fang and Stefan 2000, Leland et al. 2007, Balayla et al. 2010, Shuter et al. 2012). Fish communities will likely shift in the future towards assemblages that are intolerant of

winterkill. In North America, winterkill lakes with central mudminnows, cyprinid minnows, and yellow perch as their primary species will likely shift to assemblages dominated by centrarchids and large piscivores like largemouth bass, walleye, and northern pike, while those in Europe and Asia will likely shift in similar ways. The other biological aspects of the lakes will shift as well, with zooplankton and phytoplankton populations shifting in response to increases in planktivore and/or piscivore populations (Jackson et al. 2007, Balalya et al. 2010). The future of lakes and their response to changing winter conditions and winter kills is uncertain; understanding the effects of winterkill will help researchers and policymakers to help protect lakes and their organisms in the face of an altered world.

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Figures

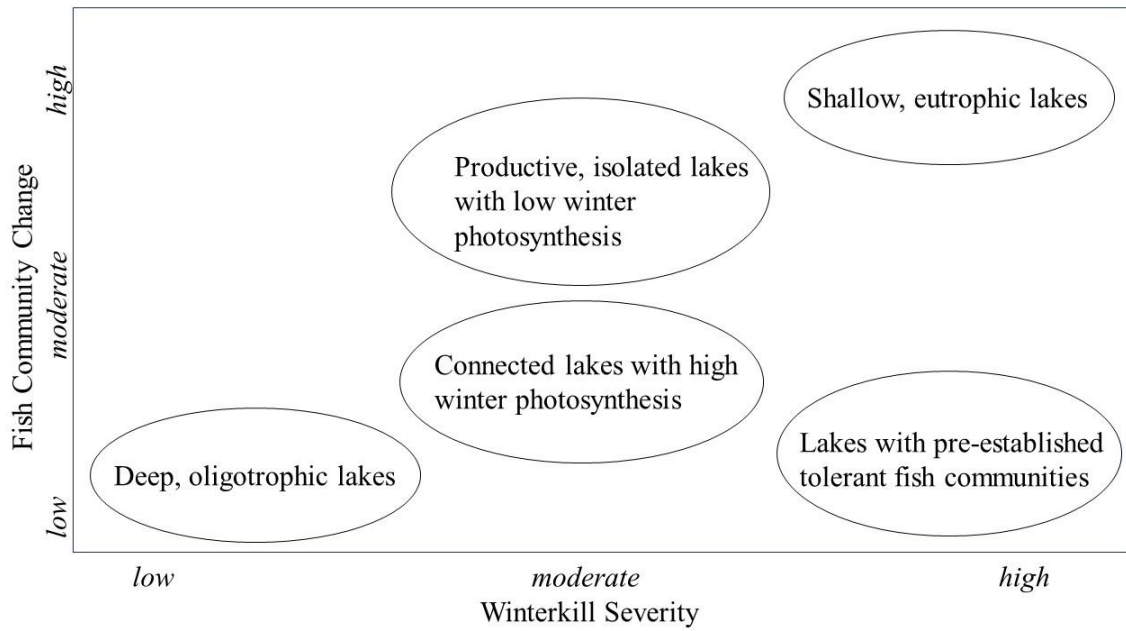


Figure 1-1. The theoretical effects of how lake characteristics and winterkill severity impact fish community characteristics.

Chapter 2

Short and long-term effects of winterkill on the fish community of Buckskin

Lake, Vilas County, Wisconsin

Abstract

Hypoxia is a significant source of winter mortality for freshwater fish in north-temperate lakes and has the potential to alter fish communities. A multi-year dataset on Buckskin Lake, a shallow, productive drainage lake in northern Wisconsin with a history of winterkill, allowed the investigation of the effects of periodic winter hypoxia on fish communities. An aeration system was installed in 1984, which raised winter oxygen levels to levels sufficient for higher fish survival. In the winter of 2007-2008, the aerator system failed, causing an extensive winterkill. The lake was sampled from 2002-2005, before the aerator failure, and in 2008-2009, after the winterkill event. In addition, 16 similar lakes in the area with no winterkill history were sampled using similar methods. Using the combined datasets, two hypotheses were tested with non-metric multidimensional scaling (NMDS) and PERMANOVA analyses. We hypothesized that (1): after 18 years of aeration, the Buckskin Lake fish community from 2002-2005 would be similar to the non-winterkill lakes due to the recolonization of species from connected lakes, and (2): the fish community changed significantly in the lake due to the 2007-2008 winterkill event. The first hypothesis was not supported, as NMDS and PERMANOVA analyses showed that Buckskin Lake retained a fish community distinct from the non-winterkill lakes. Our findings were consistent with the second hypothesis: an incomplete winterkill occurred in 2007-2008 due to lack of aeration, causing changes in fish abundances, including the reduction of game fish species and centrarchids, with no notable extinctions. Together, our findings indicate that winter aeration may improve gamefish survival and allow lakes with winterkill tendency to support sport fish

communities with healthy piscivore populations such as walleye and largemouth bass, which would be otherwise greatly reduced.

Introduction

Hypoxia is a major source of mortality for freshwater fish during the winter in north-temperate lakes (Greenbank 1945, Ultsch 1989). The severity of hypoxia can depend on many factors, including lake depth, trophic status, winter season length, and the depth of ice and snow covering a lake (Greenbank 1945, Matthias and Barica 1980). A combination of these factors can reduce oxygen to lethal levels during the winter season, leading to massive die-offs of multiple fish species in extreme cases. Long, cold, and snowy winters tend to result in more severe hypoxic conditions due to the reduction in light penetration for photosynthesis. Ice cover also acts as a barrier between the air-water interface, preventing remixing of oxygen into the water by wind action (Meding and Jackson 1980). This barrier effectively isolates oxygen present prior to ice over for the rest of winter. When winters are cold, ice cover remains longer, increasing the time before spring mixing (Fang and Stefan 2000). Photosynthesis by phytoplankton in years with less snow and clear ice cover can increase oxygen in the top layer of a lake, helping to keep oxygen levels at sufficient levels for fish survival (Greenbank 1945, Cooper and Washburn 1949).

Eutrophic lakes, which contain high amounts of nutrients and primary production, are particularly prone to winterkill. Large quantities of organic matter accumulate in the sediment of the lake and are decomposed by bacteria that consume oxygen (Mathias and Barica 1980, Babin and Prepas 1983, Danylchuk and Tonn 2003). Given that lakes during

the winter are sealed off from atmospheric oxygen, a high rate of respiration can quickly deplete oxygen in these eutrophic systems, lowering oxygen to lethal levels for fish.

Shallow lakes are also more prone to winterkill, as their smaller volume results in a lower capacity to store oxygen when ice sets in (Mathias and Barica 1980, Meding and Jackson 1980, Rahel 1984, Barica et al. 1983, Tonn et al. 1990, Clilverd et al. 2009, Balayla et al. 2010, Shuter et al. 2012).

Fish have evolved a number of adaptations to help them survive low-oxygen winter conditions. Some species swim to the ice interface in winter to access increased oxygen concentrations there produced via photosynthesis (Magnuson et al. 1985, Ultsch 1989, Shuter et al. 2012). There, they can survive even if concentrations below are completely anoxic. Fish may also increase their ventilation rate to uptake more oxygen (Lewis 1970, Davis et al. 1975, Gee et al. 1978). Some Cyprinid species can breathe microbubbles present just under the ice, giving them access to additional oxygen (Klinger et al. 1982, Magnuson et al. 1983). Also, if stream connections are present, some fish species will move into the lake outflow or the stream itself to take advantage of the higher oxygen concentrations there (Magnuson et al. 1985, Shuter et al. 2012).

Freshwater fish species demonstrate a wide range of tolerances to hypoxia. Fish in the family Salmonidae fare poorly in low-oxygen conditions. They typically live in streams or deep lakes where oxygen is readily available, and do not adapt when oxygen levels are critical (below 3 mg/L oxygen, Cooper and Washburn 1949, Davis 1975, Gee et al. 1978). Members of the Centrarchidae family also do not cope well in low oxygen conditions, below about 1 mg/L oxygen (Cooper and Washburn 1949, Petrosky and Magnuson 1973, Hail and Ehlinger 1989, Tonn et al. 1990, Farwell et al. 2007). Members

of the Percidae family vary in tolerance; with walleye (*Sander vitreus*) tolerating low oxygen less (down to 2.0 mg/L) than yellow perch (*Perca flavescens*, 0.3 mg/L, Cooper and Washburn 1949, Davis 1975). Esociform fish tolerate low oxygen well, with tolerances down to about 0.5 mg/L oxygen (Cooper and Washington 1949, Petrosky and Magnuson 1973, Klinger et al. 2012, Magnuson et al. 1983, Tonn and Paszkowski 1986, Shuter et al. 2012). Fish in the family Cyprinidae are generally very well adapted to low-oxygen conditions, tolerating concentrations of 0.2 mg/L or lower (Cooper and Washburn 1949, Davis 1975, Gee et al. 1978, Rahel 1984, Magnuson et al. 1985). Members of the catfish family Ictaluridae also do quite well in low-oxygen conditions, surviving in concentrations of 0.2 mg/L or less (Cooper and Washington 1949, Rahel 1984).

Glacial lakes in the northern hemisphere exist along a successional gradient from deep, oligotrophic lakes to shallow, eutrophic bogs (Lindeman 1942, Rahel 1984). Eutrophic lakes tend to have higher occurrences of winter hypoxia. This gradient, along with numerous ecological factors and the differing responses of fish species to hypoxia, can lead to distinct fish communities in places that experience winter hypoxia. There are two primary fish community groups shaped by winter kill that have been identified in northern Wisconsin. The first group consists of centrarchids, northern pike (*Esox lucius*), bullheads (genus *Ameiurus*), and yellow perch, while the other contains more oxygen-tolerant species like central mudminnows (*Umbra limi*), cyprinid minnows, and yellow perch (Tonn and Magnuson 1982, Rahel 1984, Tonn et al. 1990).

These fish communities may be transitional or temporary, depending on the severity of the winterkill and the connectivity to other lakes. When winterkill is frequent, they lead to sustained community types. However, if winterkills are partial, or if lakes are

well connected to others in their watershed, species recovery can occur quite rapidly, sometimes within a few years (Tonn and Paszkowski 1986, Ruuhijarvi et al. 2010). Species recovery also depends on conditions like nutrient levels in the lake, angling pressure, and macrophytes that can provide refuge to young fish (Ruuhijarvi et al. 2010).

A multi-year dataset from Buckskin Lake, a shallow, productive drainage lake in northern Wisconsin with a history of winterkill events, allowed investigation of the effects of periodic winter hypoxia on fish communities. In 1984, an aeration system to prevent winter hypoxia was installed and raised winter oxygen concentrations to sufficient levels for fish to survive even the harshest winters. In 2007-2008, the aeration system failed, allowing oxygen levels to plummet and causing an extensive winterkill event. Fish community assessments were performed in Buckskin Lake in 2002-2005 (before the winterkill event) and 2008-2009 (after the event).

An extensive dataset on fish community characteristics in 16 drainage lakes similar to Buckskin Lake in the same region allowed comparison of fish communities among the lakes. The other lakes examined have no history of winterkill except for a partial winterkill on White Birch Lake four years before the dataset was collected. Lakes in the dataset have stream connections to other lakes present and high conductivity (measured in microsiemens) indicating significant groundwater inputs. Lakes in this category have diverse and similar fish communities (Riera et al. 2000 and Hrabik et al. 2005). Biological and physical characteristics of the selected lakes fall within similar ranges. These similarities leave winterkill on Buckskin Lake as the independent condition to be explored through statistical analysis. The following hypotheses were explored using

both the multi-lake dataset as well as the 2002-2005 and 2008-2009 dataset on Buckskin Lake.

Hypothesis 1: Buckskin Lake in 2002-2005 had been successfully aerated for 20 years, possibly enabling intolerant fish species to recover from pre-1984 winterkill conditions or immigrate to the lake through stream connections. The fish communities of Buckskin Lake could therefore resemble communities found in similar lakes that do not experience winterkill. Non-metric multidimensional scaling (NMDS) analyses were performed on the drainage lake and Buckskin fish communities to determine potential differences resulting from winterkill. PERMANOVA analyses were also performed to determine significance of the differences. We hypothesized that Buckskin Lake would not significantly differ in fish community characteristics, both in terms of species presence-absence and relative abundance, from the non-winterkill drainage lakes. The elevated oxygen from aeration would allow fish species to recover from previous winterkill years. Alternatively, Buckskin Lake could differ significantly in fish community in both species presence-absence and relative abundance.

Hypothesis 2: A winterkill event occurred in Buckskin Lake during the winter of 2007-2008, potentially changing the fish communities within the lake. NMDS and PERMANOVA analyses were used to compare the species composition before and after the winterkill. We hypothesized that the fish community significantly changed in Buckskin Lake owing to this event. Species intolerant of low oxygen (specifically centrarchids and walleye) were expected to decrease in abundance or be extirpated.

Alternatively, Buckskin Lake communities could be similar in pre and post-winterkill fish communities, and would be similar to other non-winterkill lakes.

Methods

Study Site

Buckskin Lake is a 2.6 km² lake located in northern Wisconsin on the border of Vilas and Oneida counties. The lake is shallow, with a maximum depth of 7.6 m; the majority of it lies in the littoral zone, with few areas below 3 m deep (Wisconsin Department of Natural Resources 2022). The lake also has relatively high amounts of primary productivity. Buckskin Lake is located at the head of its watershed, connected via Buckskin Creek to the next lake, Amber (previously Squaw) Lake. From 1984 onward, the lake had an aeration system operated by the Buckskin Lake Association to prevent winterkill, as its shallow and productive nature made it vulnerable to oxygen loss in the winter (Thomas Hrabik, personal communication, 2023). The aeration system was effective in raising oxygen levels sufficient for fish survival. However, in 2007, the aeration system failed, preventing it from properly dispersing oxygen into the lake. In the winter of 2007-2008, oxygen conditions became severely hypoxic in the lake, creating a winterkill.

Data collection

Fish in Buckskin Lake were collected in the lake by electrofishing, fyke nets, and vertical gillnets to obtain a representative population of both pelagic and near-shore fish assemblages (see Hrabik et al. 2005 for extensive description of methods). Fish were identified to species and measured for weight and length. Alkalinity, pH, conductivity,

and total phosphorus were measured at 1 m below the surface. Secchi depth was determined, along with profiles for temperature, dissolved oxygen, and chlorophyll.

Fish abundances and environmental variables for the multi-lake dataset were collected and compiled by Hrabik et al. (2005). Similar methods were used to collect fish and environmental specimens for all lakes including Buckskin Lake. A key for drainage lake name acronyms is located in Table 2-1. The fish species richness (number of species present) in each lake is in Table 2-2. A table of what fish species are present in each study lake is in Appendix 1.

Statistical Analyses

Two metrics were used to investigate fish community differences. Species abundance data from the 16 drainage lakes and the six years of Buckskin Lake (2002-2005, four years of pre-winterkill condition, and 2008-2009, post-winterkill condition) was transformed by rooting to the $\frac{1}{4}$ power to normalize distributions. The second metric was the presence or absence of each fish species in each lake or year. For presence-absence, a 0 in a data cell corresponded to an absence of a species on a lake, while a 1 corresponded to a presence of a species. Only electrofishing was used for the abundance data on Buckskin Lake, as no other methods of fish collection were used after 2002.

Nonmetric Multidimensional Scaling

Nonmetric Multidimensional Scaling (NMDS) analyses were performed with the VEGAN package in R statistics for the two metrics (relative abundance and presence-absence). NMDS is useful for comparing large datasets of species distributions as it compresses multiple dimensions of ecological distance into only two or three dimensions. Groupings of the three lake categories (drainage, 2002-2005 Buckskin, and 2008-2009

Buckskin) were visually examined to investigate how the lakes compared in all three metrics. If lakes were similar in species abundance or presence, they would group together. These visualizations helped to explore both hypotheses 1 and 2. All NMDS figures had two dimensions- NMDS axis 1 (the x-axis) and NMDS axis 2 (the y-axis). The NMDS diagrams were created with the ‘vegan’ and ‘ggplot2’ packages in R statistics version 4.2.2. Fish species vectors were included in the diagrams to show the relative contribution of each species to the two axes. Each NMDS plot accounted for approximately 40% of the total variance in fish communities, and the stresses (an indication of the wellness of fit) fell between 0.1 and 0.2 (Table 2-3).

Bray-Curtis distance matrices were used to create the NMDS figures. This non-parametric method of creating distance matrices normalizes data by finding proportional dissimilarities. A lower value indicates more similar data (the value range is between 0 and 1). A value closer to one indicates a larger dissimilarity between two points. Bray-Curtis distances are widely used in species distribution comparisons as they can help to normalize skewed data.

Permutational Multivariate Analysis of Variance

Permutational Multivariate Analysis of Variance (PERMANOVA) statistical tests were run on all three metrics to determine differences among groupings between the different lake categories. The analysis was done using the VEGAN package in R statistics. PERMANOVA is a non-parametric test that uses ranked similarities to compare centroid distributions between categories. The null hypothesis is that centroid distributions are equivalent (i.e., that the distributions seen in groups of data are randomly distributed). If the p-value is below a certain threshold (in this study >0.05), then the null

hypothesis is rejected; centroids are not equivalent, and data is not randomly distributed (Anderson and Walsh 2013). Non-significant results point to no discernable differences seen between categories, while significant results point to discernable differences detected. Significance for all of the PERMANOVA tests was determined at the $\alpha=0.05$ level. Permutations sufficient to obtain relevant significant figures were used for each PERMANOVA, the minimum number of permutations being 719.

Five PERMANOVA tests were performed for each metric. Four tests were done on the different combinations of Bucks skin and drainage lakes (all three categories, drainage and combined Bucks skin years, pre-winterkill Bucks skin and drainage, and post-winterkill Bucks skin and drainage) to investigate hypothesis 1. Non-significant differences in the tests supported hypothesis 1. The last test compared pre and post-winterkill Bucks skin years for hypothesis 2. Significant differences in this test would support the hypothesis.

Similarity Percentage (SIMPER)

SIMPER (similarity percentages) analyses were conducted on the two metrics (relative abundance and presence absence) to determine how much each fish species contributed to any dissimilarities seen between the pre-winterkill Bucks skin years and the non-winterkill lakes. The VEGAN package in R statistics was used for the SIMPER analyses, which uses Bray Curtis distances to determine the contribution of each fish species. Fish species contributions would help explain why differences might occur between the two lake categories, giving more insight for hypothesis 1. Not all fish species are shown through SIMPER, as it only displays species that have cumulatively 70% contribution.

Individual comparisons in species abundance on Buckskin Lake

The abundances of ten fish species were individually compared on Buckskin Lake in the years 2002-2005 and 2008-2009. These species were yellow perch (*Perca flavescens*), walleye (*Sander vitreus*), bluegill (*Lepomis macrochirus*), pumpkinseed (*Lepomis gibbosus*), rock bass (*Ambloplites rupestris*), largemouth bass (*Micropterus salmoides*), northern pike (*Esox lucius*), bluntnose minnow (*Pimephales notatus*), golden shiner (*Notemigonus crysoleucas*), and white sucker (*Catostomus commersonii*). Other species were present but in numbers too low for comparison between years.

Environmental data

Environmental variables for all lakes and years compared were compiled, consisting of lake area (hectares), maximum lake depth (meters), lake order, total dissolved phosphorus ($\mu\text{g/L}$), chlorophyll ($\mu\text{g/L}$), and conductivity (microsiemens, μS). Average values were used for each lake and Buckskin year if multiple samples were collected. Variables were integrated into the NMDS graphs, providing a visualization of environmental relationships to fish community composition. The variables vectors plotted on the NMDS do not relate to a direct numerical relationship, as they are constructed from ranked similarities, but do offer insight into how environmental variables impacted the fish communities observed.

Results

Comparison of multiple lakes

The NMDS analyses of both relative abundance (Figure 2-1) and presence-absence (Figure 2-2) grouped the pre-winterkill (2002-2005) Buckskin Lake fish

community separately from the other drainage lakes. The separations appeared quite clear for most of the groupings, with the drainage lakes grouped closer to the negative side of NMDS axis 1, and the pre-winterkill Buckskin years grouped to the positive side. A notable exception to the drainage lakes was White Birch Lake, which grouped close to the pre-winterkill Buckskin years in relative abundance (Figure 2-1) and presence-absence (Figure 2-2). This lake had suffered a partial winterkill four years prior to sampling.

PERMANOVA tests for both relative abundance and presence-absence revealed significant differences in fish community groupings for the pre-winterkill Buckskin years compared to the drainage lakes (Table 2-4). When the four pre-winterkill and two post-winterkill years were grouped together and compared to the drainage lakes, significant differences were identified in both metrics. PERMANOVAs on all three categories grouped separately also found significant differences.

SIMPER analysis for relative abundance found that bluegill, smallmouth bass, and bluntnose minnow contributed the most to the difference between pre-winterkill Buckskin and the non-winterkill lakes, while smallmouth bass, black crappie, and common shiner were the most contributive to the presence absence difference (Table 2-5). No one species had a dominant contribution to the differences seen, with the highest contribution being about 8 percent (Table 2-5).

Effects of winterkill on Buckskin Lake

NMDS plots comparing pre and post-winterkill fish communities in Buckskin Lake showed unique communities for each condition in both relative abundance and presence-absence. The relative abundance metric placed the two post-winterkill years

closer to the drainage lakes than the pre-winterkill years, but the separation was not striking (Figure 2-1). The presence-absence NMDS analyses put all Buckskin Lake sample years close together, with the post-winterkill years overlapping the pre-winterkill years (Figure 2-2).

PERMANOVA tests comparing pre and post-winterkill Buckskin years gave mixed results. PERMANOVAs comparing Buckskin as a whole (pre and post-winterkill) to the drainage lakes found significant differences in fish communities for all metrics, along with those comparing all three categories to each other (Table 2-4). However, when pre-winterkill Buckskin was compared to post-winterkill Buckskin, the presence-absence metric found no significant differences. The relative abundance metric had a lower p-value than presence-absence (0.133, Table 2-4), but was also not significantly different. The post-winterkill Buckskin community was significantly different from the other drainage lakes in relative abundance and presence-absence metrics.

Several fish species changed in abundance in Buckskin Lake from before to after the 2007-2008 winterkill event. Yellow perch varied greatly in abundance in the years between 2002-2005, with a large change observed in 2004 (Figure 2-3). After the winterkill event, the abundance increased, with an approximately ten-fold increase in 2008 and 2009 compared to 2005. Walleye were also variable in abundance from 2002-2005, with a large reduction in number seen after the winterkill event. Many bluegill were observed in 2003 and 2009; there were no discernable patterns seen from before to after the winterkill event. Pumpkinseed were variable in abundance in all years; no clear pattern was seen in association with the winterkill event. Rock bass generally decreased in abundance after the winterkill, with less than half of the number seen in 2008 and 2009

compared to 2002-2005. Bluntnose minnows increased from the 2002-2005 period to 2008-2009. Golden shiner increased slightly in abundance from before to after the winterkill. White sucker generally increased from before to after the winterkill event. However, white suckers in 2005, before the winterkill, had a similar number to 2008 and 2009.

NMDS fish species vectors

For the among lake relative abundance NMDS analyses, the most influential species on NMDS axis 1 were rosyface shiner (*Notropis rubellus*), spottail shiner (*Notropis hudsonius*), and trout perch (*Percopsis omiscomaycus*), all with a negative relationship with the axis (Figure 2-1). For the NMDS axis 2, lake whitefish (*Coregonus clupeaformis*) and lake trout (*Salvelinus namaycush*) were most positively influential, while black bullhead (*Ameiurus melas*) were most negatively influential. For presence-absence, NMDS axis 1 was most influenced by trout perch, rosyface shiner, and spottail shiner, all negatively (Figure 2-2). Black bullhead had a strong positive relationship with NMDS axis 2, while lake trout and lake whitefish had a strong negative relationship.

Environmental Variables

Buckskin Lake in all years fell within the environmental variable ranges seen in the group of drainage lakes (Table 2-6). However, specific conductance, along with phosphorus and chlorophyll, two indicators of productivity, were higher in values when compared to the other drainage lakes, consistent with Buckskin being a more productive lake.

Environmental vectors on the NMDS graphs followed the same general pattern regardless of the metric (relative abundance and presence-absence). Phosphorus and

conductance were positively correlated with NMDS axis 1, with those further on the upper right generally being more eutrophic. Lake order was negatively associated with NMDS axis 1, with drainage lakes of a higher order generally resembling Buckskin Lake less. Conductivity was negatively correlated with NMDS axis 1, while lake depth was positively correlated with NMDS axis 1; however, as both vectors were mostly associated with NMDS axis 2, neither seemed to impact the relatedness of Buckskin compared to the drainage lakes much, which primarily separated along axis 1.

Discussion

Multi-lake comparison

Our findings show that Buckskin Lake, prior to the winterkill event in 2007-2008, had a unique fish community when compared to the nearby non-winterkill drainage lakes, which was evident in the NMDS analyses and the significance of the PERMANOVA tests. Analyses of NMDS relative abundance and presence-absence show that Buckskin Lake in 2002-2005 grouped separately from the other drainage lakes, with the exception of White Birch Lake, which had a history of a partial winterkill. The consistency of groupings regardless of metric provides additional support for the validity of the differences observed. These differences primarily occurred along NMDS axis 1. PERMANOVA results were consistent with NMDS groupings, with significant differences seen between pre-winterkill Buckskin and the other drainage lakes regardless of metric or category combined.

Overall, our results did not support hypothesis 1, which posited that there were no discernable differences between Buckskin in 2002-2005 and the other drainage lakes.

Buckskin Lake in 2002-2005 had a distinct fish community compared to other lakes around it that did not experience winterkill, with the exception of White Birch Lake, a lake with partial winterkill shortly before sampling. It appears that, although aeration successfully raised oxygen to sufficient levels for fish survival in the winter, a legacy of winterkill on the lake nonetheless likely persisted twenty years after its installation.

A unique fish community in Buckskin Lake possibly due to winterkill conditions, even in the presence of an aerator for many years, is consistent with the findings of other investigations. In other studies of lakes in Northern Wisconsin, distinct fish communities are seen in association with winterkill, although the lakes have very different environmental conditions (Tonn and Magnuson 1982, Rahel 1984, Tonn et al. 1990). The winterkill conditions on these lakes occurred over many years, leading to only tolerant fishes remaining in the lakes. Buckskin Lake, like these other studies in Wisconsin, has a unique fish community, both through the species present and their relative abundances. However, the characteristics of the lakes studied in the other Wisconsin studies differ from Buckskin and the drainage lakes of this study. Species intolerant of low winter oxygen like walleye, rock bass, and bluegill are present in Buckskin Lake; these fish are rare or absent in the other winterkill studies. Other winterkill lakes examined are generally smaller and more acidic than Buckskin, leading to possible variations in the exact species and conditions present. While this makes direct comparisons difficult, it illustrates a broader context in which winterkill might shape fish communities. Rather than just being relegated to small and possibly acidic lakes, winterkill could also significantly impact larger lakes that have fish immigration routes from other bodies of water. The headwater position of Buckskin Lake and its unique fish community may

reflect other studies that find that more isolated lakes often have lower species diversity and a harder time recovering from extinction events (Kratz et al. 1997, Shuter et al. 2012). The position of Buckskin Lake at the head of its watershed may mean that fish had a difficult time migrating from other lakes, as with other isolated lakes. Even with sufficient winter oxygen provided by the aerator for many years, fish species that were eliminated by past winterkill events may not have enough time to migrate from lakes further down in the watershed, leaving only more tolerant species present. The ecological conditions of the lake could also have been altered compared to lakes that did not have winterkill; short-term and long-term alterations of ecological conditions and biological communities after winterkill events have been documented in other lakes in Europe and North America (Hail and Ehlinger 1989, Bronmark and Weisner 1992, Tessier and Woodruff 2002, Jeppesen et al. 2004, Tonn et al. 2004, Jackson et al. 2007, Balayla et al. 2010, Ruuhijarvi et al. 2010, Hilt et al. 2014). The aeration system, although it did raise levels to sufficient levels for fish, perhaps did not raise it enough for low-oxygen intolerant fish species to thrive. As fish have a range of tolerances, a moderate amount of oxygen could mediate the amount of low-oxygen intolerant fish present. Although not all the fish may be killed outright in a moderate oxygen scenario, the quality of habitat characteristics of these fish may be reduced when in sub-optimal levels for several months, preventing optimal growth and reproduction necessary to maintain high levels of abundance.

While winterkill may have led to the unique fish population on Buckskin Lake, alternative reasons could explain the differences in fish community seen. SIMPER results had a variety of low-oxygen tolerant and intolerant species contributing to the differences

between Buckskin Lake and the non-winterkill lakes, and no one species dominated in contribution. Additionally, some species vectors for the NMDS figures were opposite of what would be expected of Buckskin being shaped by winterkill alone, with tolerant minnow species pointing away from Buckskin and intolerant species like walleye pointing towards it. If winterkill were the sole reason for the difference in fish community, there would likely be large contributions of yellow perch and minnow species, which are both emblematic of winterkill lakes, and tolerant species vectors would point away from Buckskin Lake, the opposite of what was observed. Multiple other factors like summer fish kill, human disturbance, stocking of fish species, or the geographical isolation of Buckskin Lake could be contributing to the unique fish population in addition to or instead of winterkill. Summer fish kill involves low oxygen concentrations in the growing period due to large amounts of organic matter breakdown; it could result in die-offs of certain species, but perhaps in different ways than winterkill would. Human impacts tend to increase the amount of disturbance on a lake and the removal of large predator species like walleye and northern pike; both of these factors could result in a change in fish community not characteristic of winterkill. Finally, while geographical isolation can increase the potency of winterkill effects on fish communities, it can also act by itself and in combination with other factors to make unique fish communities. Buckskin Lake has a smaller number of fish species on it than many of the other lakes compared (Table 2-2); this lack of diversity could help explain the differences seen in the statistical methods.

Effects of winterkill on Buckskin Lake

Our observations are with an incomplete winterkill on Buckskin Lake in 2007-2008. Abundances of several species changed, but there were not any notable extinctions of species between the pre and post-winterkill years. The winterkill conditions were perhaps severe enough to reduce some low-oxygen intolerant fish like walleye and rock bass, but not severe enough to cause extirpation. The intolerant fish could have survived in the top layer of the lake, which did have oxygen present (up to 2.2 mg/L oxygen in the first two meters). This oxygen could have been provided either by photosynthesis or by the limited action of the aerator in that year. The fish also could have moved to the stream outlet present in the lake, allowing them to wait out anoxic conditions. However, the intolerant fish were not able to completely escape their fate. The low-oxygen tolerant species appear to have been resistant to the winterkill. Yellow perch and other tolerant species could have had a greater number of offspring survive in the years after the winterkill, as intolerant species would be reduced in number, providing tolerant offspring with a lower chance of predation and a higher food supply.

On other lakes with winterkill, fish abundances greatly change, shifting from dominance by low-oxygen intolerant fish to tolerant species, especially to those that are the young-of-year born from those tolerant fish in the spring following a winterkill event (Tonn and Paszkowski 1986, Hail and Ehlinger 1989, Ruuhjarvi et al. 2010, Hilt et al. 2014). Buckskin Lake did experience a decrease in intolerant species (walleye, rock bass) and an increase in tolerant fish species (yellow perch, bluntnose minnow). Presumably, the increases in yellow perch and bluntnose minnow could be due to large numbers of those species born in the spring of 2008 that thrived free of competition or predation from walleye or centrarchids. However, the changes overall were not significant, contrasting

somewhat from earlier studies. Even in incomplete winterkills, extinctions of especially vulnerable species can occur; this was not observed in Buckskin Lake (Ruuhjarvi et al. 2010, Hilt et al. 2014). Species that are generally intolerant of low oxygen in Buckskin Lake (i.e. walleye, rock bass) were still present after the winterkill.

Environmental variables

Phosphorus and chlorophyll were relatively high in winterkill-prone Buckskin Lake compared to the other drainage lakes. This is consistent with previous studies, which found that eutrophic lakes have higher rates of winterkill due to high rates of organic decomposition. The other factor associated with high amounts of winterkill, shallow depth, also seemed to be somewhat correlated to the groupings of the winterkill lakes, as deeper lakes occurred further away from Buckskin Lake and White Birch Lake.

Limitations of the study

There are several limitations associated with this study. Although the lakes used in the study were fairly similar in their environmental factors, there could be additional, unexplored variables associated with the fish assemblages present in the lakes included in this study. Even though the lakes were selected to reduce variability, environmental factors varied with some lakes having ten times the level of one factor than others. As an example, total phosphorus ranged from 3 to 30 $\mu\text{g/L}$ among the selected lakes (Table 2-6). This nutrient often limits primary production in lakes, and variations in this could have large impacts on resident fish communities.

The fish communities in Buckskin Lake before 2002 are unknown. This prevented us from assessing both what the fish community was before installation of the aerator as well as how the community in the lake evolved in the years after its installation. This

limited the time scale for which interpretation was impossible, and only provided a modest view of the fish community evolution on this lake.

Another limitation of the study is the lack of a true before-after control-impact (BACI) design. A BACI design includes at least two sites, one being a control and another which is modified; both are measured at the same time before and after the modification (Seger et al. 2021). This design can help to increase the interpretive power of a study as it decreases the amount of uncertainty from natural variations in an environment. While there was a treatment on Buckskin lake for hypothesis 1 (the aerator), no measurement was made of the fish community before its installation, and no true control lake (unmodified and similar to Buckskin in most or all variables) was used for comparison, meaning that variations in environmental conditions could have large impacts on the fish communities that cannot be explored. Secondly, there was no control for the second hypothesis investigating Buckskin Lake before and after the 2007-2008 winterkill. A control for this part of the study would help to see if there were simply variations in the fish community due to the particulars of that specific time period; without this control no assessments on those variations could be made.

Management Recommendations

Our findings show that aeration was successful on Buckskin Lake and provided critical refuge for game fish species in the winter months. While the fish community in Buckskin Lake did differ from similar lakes even many years after the installation of the aerator, it nonetheless retained large populations of walleye and other game fish.

Expanding the aerator would allow for more oxygen to remain in the lake during winter,

and could prevent winterkill events like that seen in 2007-2008 from reducing or eliminating game fish populations.

Conclusion

It is clear that Buckskin Lake has a unique fish community due to winterkill even after many years of winter aeration. The isolation of the lake and the difficulty of repopulating a lake with fish species less tolerant of low oxygen likely contributed to this distinct fish community. An incomplete winterkill occurred in 2007-2008 due to reduced aeration, with changes in fish abundance but no known extinctions, although game fish species and centrarchids were greatly reduced. These changes resemble those observed in other lakes, with large new year-classes of tolerant fish born in the spring following the winterkill (Ruuhjarvi et al. 2010, Hilt et al. 2014). Future research on Buckskin Lake could investigate changes in the fish community in the years since the 2007-2008 winterkill event to document species recovery. Other large, neutral pH lakes in the area with a history of winterkill could also be identified and included in a study to more broadly determine the effects of winterkill on large lakes in northern Wisconsin and elsewhere.

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Figures and Tables

Table 2-1. Lake abbreviations and formal names key

Acronym	Lake Name	Acronym	Lake Name
AH	Arrowhead	LK	Lower Kaubashine
AL	Allequash	RO	Round
BG	Big	TR	Trout
BO	Boulder	UK	Upper Kaubashine
BR	Brandy	WB	White Birch
BS	Buckskin	WC	Wildcat
IS	Island	WR	Wild Rice
JO	Johnson	WS	White Sand
LC	Little Crooked		

Table 2-2. Fish species richness (number of fish species present) in each study lake

Lake	Species Richness	Lake	Species Richness
AH	16	RO	18
AL	17	TR	16
BG	17	UK	16
BO	15	WB	11
BR	17	WC	19
IS	16	WR	22
JO	19	WS	17
LC	18	BS	12
LK	20		

Table 2-3. NMDS stress and variance explained values.

Metric type	Stress	% variance explained (NMDS axis 1)	% variance explained (NMDS axis 2)
Relative abundance	0.149959	22.7	18.4
Presence Absence	0.1256323	27.8	16.9

Table 2-4. Summary of PERMANOVA statistics for the two metrics (Relative abundance and presence-absence). “Lakes compared” describes groupings compared. “Non, pre, post” compared all three categories of lakes (drainage lakes, 2002-2005 pre-winterkill Buckskin, and 2008-2009 post-winterkill Buckskin). “Non, buckskin” compared drainage lakes to all six Buckskin years grouped together. “Non, pre” compared drainage lakes and 2002-2005 pre-winterkill Buckskin years. “Non, post” compared drainage lakes and 2008-2009 post-winterkill Buckskin years. “Pre, post” compared the 2002-2005 pre-winterkill Buckskin years and the 2008-2009 post-winterkill Buckskin years. Asterisks in the p-value column designate significance at the $\alpha=0.05$ level.

Metric	Lakes compared	Degrees of freedom	F value	P-value
Relative abundance	non, pre, post	21	3.5722	>0.001*
	non, buckskin	21	6.3188	>0.001*
	non, pre	19	5.4259	>0.001*
	non, post	17	1.9838	0.040*
	pre, post	5	1.9703	0.133
Presence absence	non, pre, post	21	4.7611	0.002*
	non, buckskin	21	9.7338	>0.001*
	non, pre	19	6.9895	>0.001*
	non, post	17	3.0578	0.019*
	pre, post	5	0.5741	0.667

Table 2-5. Contribution of each fish species to differences observed between Buckskin Lake pre-winterkill and non-winterkill lakes for both metrics (relative abundance and presence absence) through SIMPER analysis.

Relative Abundance		Presence Absence	
Species	Percent contribution	Species	Percent contribution
Bluegill	7.90	Smallmouth Bass	7.58
Smallmouth Bass	7.36	Black Crappie	7.49
Bluntnose Minnow	5.85	Common Shiner	7.30
Black Crappie	5.62	Mimic Shiner	5.64
Yellow Perch	5.42	Golden Shiner	5.10
Mimic Shiner	5.30	Blackchin Shiner	4.93
Common Shiner	4.69	Bluntnose Minnow	4.78
Pumpkinseed	4.47	Muskellunge	4.65
Cisco	4.10	Northern Pike	4.60
Golden Shiner	4.03	Log Perch	4.59
Largemouth Bass	3.92	Shorthead Redhorse	4.44
Blackchin Shiner	3.58	Cisco	4.06
Shorthead Redhorse	3.25	Blacknose Shiner	3.88
Walleye	3.13	Hybrid Sunfish	3.35
Blacknose Shiner	3.07	(Bluegill and Pumpkinseed)	

Table 2-6. Summary of environmental characteristics for drainage lakes and in Buckskin in the years 2002-2005 and 2008-2009. 2002 data was used for 2003-2005 Buckskin years for phosphorus and chlorophyll, and an average of 2008 and 2009 for conductivity was used for Buckskin in 2002-2005. Units measured are lake area (acres), maximum depth (meters), total dissolved phosphorus ($\mu\text{g/L}$), chlorophyll ($\mu\text{g/L}$), and conductivity (microsiemens, μS).

Lake name	Area (hectares)	Lake Order	Maximum depth (meters)	Chlorophyll ($\mu\text{g/L}$)	Phosphorus ($\mu\text{g/L}$)	Conductivity (μS)
IS	757	4	35	9.3	21.67	98
JO	78	3	42	5.2	11	175
BG	850	3	61	4.2	9.33	129
RO	116	3	28	9.1	15	116.5
WR	365	3	26	9	15.67	93
BO	525	3	23	13.1	23	76.5
BR	110	2	44	3.8	15.5	175
LC	153	2	20	5.5	19.3	120
MD	214	2	18	6.4	30	113
TR	3864	2	117	3.23	3	98
WS	728	2	71	2.1	6	76
WB	117	2	27	4.2	14.3	59
WF	393	1	28	10.6	45	134
LK	187	1	36	2.2	11	121
AL	405	1	37	6.7	12.67	95
WC	316	0	38	12.4	16.7	179
UK	182	0	58	1.4	9.33	99
AH	99	0	45	6.75	12	95
BS02	642	0	22	11.02	24.09	93.9
BS03	642	0	22	11.02	24.09	93.9
BS04	642	0	22	11.02	24.09	93.9
BS05	642	0	22	11.02	24.09	93.9
BS08	642	0	22	5.54	21.2	90.6
BS09	642	0	22	6.98	27.3	97.3

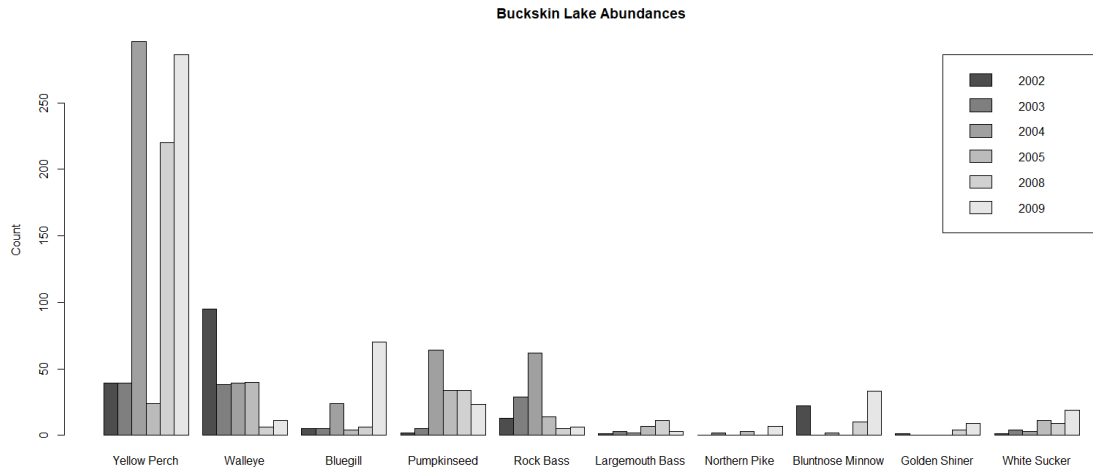


Figure 2-3. Bar graph showing species abundance found by electrofishing in six separate years on Buckskin Lake. The 2002-2005 period corresponds to the pre-winterkill period, and the 2008-2009 years occurred after the winterkill in 2007-2008. Electrofishing efforts were consistent across all years and species.

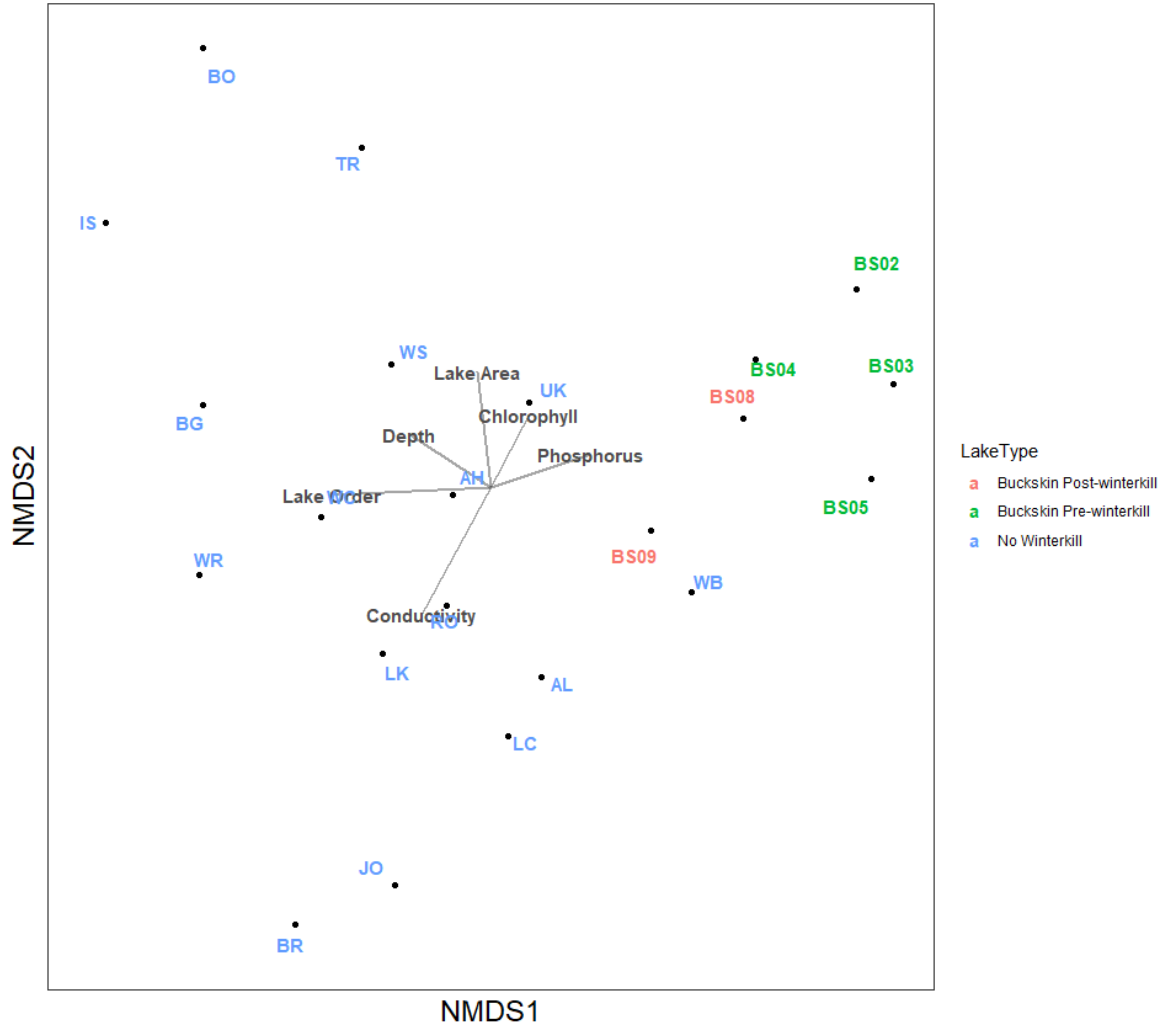


Figure 2-4. NMDS analysis of relative abundance data with environmental vectors for all lakes. “No Winterkill” indicates the 16 drainage lakes, “Buckskin Pre-Winterkill” indicates Buckskin Lake in the four years 2002-2005, and “Buckskin Post-Winterkill” indicates Buckskin Lake in the two years 2008-2009. Vectors indicate relative contribution of the environmental variables to NMDS axis 1 and NMDS axis 2.

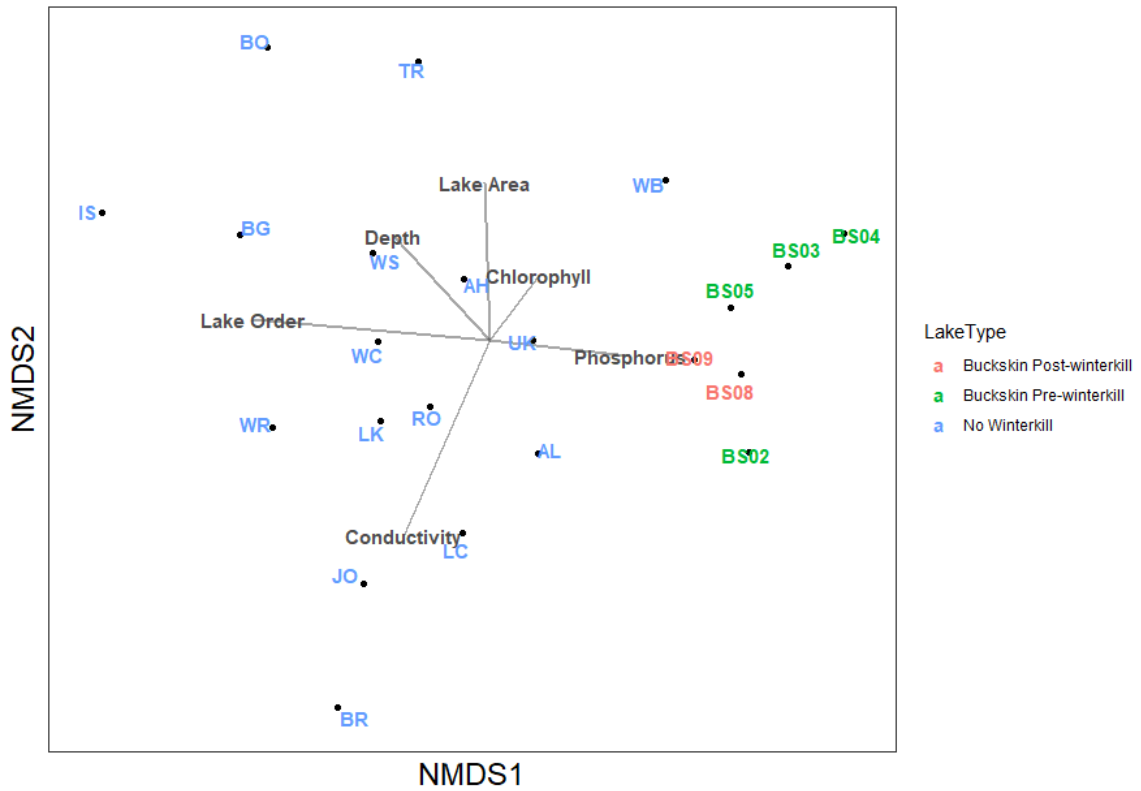


Figure 2-5. NMDS analysis of presence-absence data with environmental vectors for all lakes. “No Winterkill” indicates the 16 drainage lakes, “Buckskin Pre-Winterkill” indicates Buckskin Lake in the four years 2002-2005, and “Buckskin Post-Winterkill” indicates Buckskin Lake in the two years 2008-2009. Vectors indicate relative contribution of the environmental variables to NMDS axis 1 and NMDS axis 2.

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Appendices

Appendix 1, table 2-7. Fish species present in each lake studied. An “x” indicates the presence of a species on a lake. Lake names can be found in Table 2-1.

Species	Lake	A H	A L	B G	B O	B R	I S	J O	L C	L K	R O	T R	U K	W B	W C	W R	W S	B S
Black Bullhead						x												
Blackchin Shiner				x		x	x	x	x	x					x	x		
Black Crappie		x	x	x		x	x	x	x	x			x	x		x	x	
Blacknose Shiner		x				x			x		x				x	x	x	
Bluegill		x	x	x		x		x	x	x	x	x	x	x	x	x	x	x
Bluntnose Minnow		x	x	x	x	x	x	x	x	x	x	x	x		x		x	x
Brook Stickleback					x									x				
Burbot																		
Cisco		x		x		x	x	x				x						x
Common Shiner			x	x	x	x	x	x	x	x	x				x	x	x	
Fathead Minnow																		
Golden Shiner		x	x			x		x	x	x	x		x		x	x		x
Horny Head Club										x								
Iowa Darter			x			x		x					x		x			
Johny Darter											x		x		x			x
Lake Trout												x						
Lake Whitefish												x						
Largemouth Bass		x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x
Log Perch		x		x	x		x					x			x	x	x	
Mimic Shiner		x		x	x			x		x		x	x		x	x	x	
Mottled Sculpin					x		x	x			x		x					
Northern Pike			x			x				x						x	x	x
Pumpkinseed		x	x	x		x		x	x	x	x	x	x	x	x	x	x	x
Rock Bass		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Rosyface Shiner							x										x	
Shorthead Redhorse				x	x		x		x	x	x				x	x		
Smallmouth Bass		x	x	x	x		x			x	x	x	x	x	x	x	x	
Trout Perch				x	x							x						
Walleye		x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x
White Sucker		x	x	x	x		x		x	x	x	x	x	x	x	x	x	x
Yellow Bullhead			x			x		x	x							x		
Yellow Perch		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Rainbow Smelt																		
Muskellunge		x	x		x			x	x	x	x		x	x	x	x		x
Central Mudminnow						x		x		x						x	x	
Warmouth										x								
Spottail Shiner							x									x		
Grass Pickerel									x									
Freshwater Drum																		
Hybrid Bluegill			x	x				x	x									x
Pumpkinseed																		