From aquatic connectivity to aquatic conservation in Algonquin Provincial Park

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From aquatic connectivity to aquatic conservation in Algonquin Provincial Park

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Cover photo: Release of an adult brook trout in an Algonquin Park lake during a fish monitoring survey. Photo by Darren Smith

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Summary

Recognition of the importance of water, watersheds, and their network has been exceptional in Algonquin Provincial Park since it's establishment in 1893. The focus has been and remains aquatic connectivity and protecting the park's unique headwater landscape. However, because priorities identified in the late 19th century may not address 21st century aquatic stressors, aquatic conservation planning is needed to ensure adequate protection of the park's aquatic resources.

Aquatic conservation planning is a relatively new concept in managing watersheds and their associated fauna. Aquatic fauna and food webs are the most imperilled globally so the need for planning to conserve ecological integrity of watersheds is seen as a key step in conservation. Summarized here are information and options to consider in planning for aquatic conservation in Algonquin Provincial Park, Ontario, Canada, in the 21st century.

The park has many features that make aquatic conservation planning an important element of broader planning goals. Perhaps the most important is the historical recognition of the importance of maintaining functional headwater watersheds. Several major watersheds begin on the Algonquin Dome and drain into the Great Lakes or the Ottawa River. Because of the protection afforded these watersheds within park boundaries, this feature is a key consideration for planning. In most of the park, the native fish fauna is intact, with introduced species limited to several access areas. Algonquin Provincial Park is home to many native brook trout populations as well as the full spectrum of lake trout food web diversity observed across Ontario and the Great Lakes. Distinct cisco and lake whitefish forms are unique to the park. In most areas, the aquatic ecological integrity of the park remains high, making aquatic conservation planning a necessary next step to ensure it stays that way.

Résumé

De la connectivité aquatique à la conservation aquatique au parc provincial Algonquin

La reconnaissance de l'importance de l'eau ainsi que des bassins versants et de leur réseau est exceptionnelle au parc provincial Algonquin depuis sa création en 1893. L'accent a été mis – et il le reste – sur la connectivité aquatique et la protection du paysage unique du parc, parsemé de cours d'eau d'amont. Cependant, comme les priorités cernées à la fin du 19^{e} siècle ne correspondent peut-être pas aux agents stressants aquatiques du 21^{e}, la planification de la conservation aquatique s'impose pour assurer une protection adéquate des ressources aquatiques du parc.

La planification de la conservation aquatique est un concept relativement nouveau dans la gestion des bassins versants et de leur faune propre. La faune aquatique et les réseaux trophiques comptent parmi les plus menacés à l'échelle mondiale, d'où la nécessité de planifier pour conserver l'intégrité écologique des bassins versants – une étape clé en conservation. Sont résumées ici des données et options à considérer dans la planification de la conservation aquatique au parc provincial Algonquin, en Ontario, au Canada, au 21^{e} siècle.

Le parc a de nombreuses caractéristiques qui font de la planification de la conservation aquatique un élément au cœur des objectifs de planification plus vastes. La plus importante est peut-être la reconnaissance historique de l'importance du maintien de bassins versants d'amont fonctionnels. Plusieurs grands bassins versants commencent dans le massif Algonquin et s'écoulent dans les Grands Lacs ou dans la rivière des Outaouais. En raison de la protection dont bénéficient ces bassins versants dans les limites du parc, il s'agit d'une caractéristique clé pour la planification. Dans la plus grande partie du parc, l'ichtyofaune indigène est intacte, les espèces introduites étant limitées dans plusieurs zones d'accès. Le parc provincial Algonquin abrite de nombreuses populations d'ombles de fontaine indigènes ainsi que l'ensemble du réseau trophique du touladi dans toute sa diversité que l'on observe en Ontario et dans les Grands Lacs. Le parc se distingue par des ciscos et grands corégones uniques. Dans la plupart des zones, l'intégrité écologique de l'écosystème aquatique demeure élevée, et la planification de la conservation aquatique est donc une étape nécessaire à franchir pour qu'il en soit toujours ainsi.

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Introduction

Algonquin Provincial Park (hereafter Algonquin Park) is recognized globally as a place of unique aquatic and terrestrial ecosystems. For park visitors, travelling by portage routes among the lakes and rivers is a memorable experience because of the beauty of the landscape. The park also functions as a conservation area as it protects many headwater aquatic ecosystems and watersheds flowing off the Algonquin Dome (Ridgway et al. 2017). Native species and their supporting food webs occupy the landscapes and waterscapes of the park. Ensuring the protection of aquatic values persists for our continued enjoyment requires considering planning options for aquatic conservation. According to the Algonquin Provincial Park Management Plan of 1998 (Ontario Parks 1998), the goal of the park is "to provide protection of natural and cultural features, continuing opportunities for a diversity of low-intensity recreational, wilderness, and natural environmental experiences; and within this provision continue and enhance the park's contribution to the economic, social, and cultural life of the region." The conservation of Algonquin Park, including its organisms and ecosystems, is a high priority.

The first priority for management and planning in Ontario Parks is sustaining native, viable populations of terrestrial or aquatic predators and prey in native, functioning ecosystems. This is referred to as maintaining ecological integrity. Current planning is based on designated zones that prioritize uses: historical value protection, wilderness preservation, sustainable recreation, and development activities. Like many parks, Algonquin Park has a long history of conserving terrestrial and aquatic ecosystems and planning for their use and preservation. The original designation of the park in the 1893 Report of the Royal Commission on Forest Preservation and National Park listed "The preservation of streams, lakes and watercourses in the park, and especially of the headwaters of those rivers that have the sources therein..." (p. 23) as the first goal of the then new park. Another goal was "To serve the benefits which the retention of a large block of forest would confer upon the climate and watercourses of the surrounding portions of the Province" (p. 29). Both goals addressed the importance of watersheds, their components, and water budgets within and beyond park boundaries. The early recognition of the importance of the park's watersheds and of its unique geographic role in southern Ontario should greatly benefit future aquatic conservation in Algonquin Park.

The purpose of this report is to highlight elements of aquatic conservation planning to consider given the unique location of Algonquin Park — not to develop a plan. Aquatic conservation can take many forms and interest in the related scientific and resource management literature is growing. Here we broadly summarize the published scientific literature on aquatic conservation planning. Many elements of a modern approach to aquatic conservation planning were not considered in 1893 but are important for the future. Stressors that were not considered in the 19th century have become priorities in the 21st century. For Ontario Parks, maintaining ecological integrity is the priority, as described in the Provincial Parks and Conservation Resources Act, 2006. The act states that parks can function as points of reference in monitoring of ecological change and that restoring ecological integrity is to be considered. These are modern concepts and reflect the challenges facing aquatic conservation in Ontario.

The Algonquin Park Master Plan (OMNR 1974) updates and renews a commitment to “a headwater area of clear flowing lakes, rivers and streams; a wide variety of plants and animals...” (p. 3). One environmental goal of that plan was “to maintain the volume and quality of park waters” (p. 9). The master plan re-emphasized that “preservation of the lands and waters of the headwater highland area occupied by Algonquin has been a major consideration in the management of the park since its inception in 1893” (p. 17). Conservation of aquatic values has expanded. The Algonquin Park Management Plan Amendment (Ontario Parks 2013) identified the importance of riparian zone conservation and extended protection of this lakeshore habitat around many lakes, particularly for the conservation of native brook trout. Water, watersheds, and their network have always been at the core of the intent of Algonquin Park.

Aquatic ecosystems are defined by watershed boundaries and directional flow of water among lakes and rivers in a watershed, as originally conceived in 1893 for Algonquin Park. An aquatic ecosystem at any point in a watershed is more than the sum of its parts from upstream. It emerges as its own ecosystem because all river, stream, and lake contributions to this point cannot be separated (Melles et al. 2012, 2014). Watershed properties, such as primary production, species assemblages, and habitats, change as water flow and volume increase downstream. The streams and lakes of the park should be viewed as directional, nested networks (Ridgway et al. 2018a). Because of this network structure, species introductions in one location can be transported or disperse widely based on network connections among the park’s watersheds.

This network has a history in Algonquin Park. The effects of glaciation on the park landscape ended about 12,000 years ago. Part of the network served as the outflow of glacial Lake Algonquin as it drained through the northern regions of the park in what is now the Petawawa River (Ridgway et al. 2017b). Because of this shared drainage history, invertebrate fauna of the lakes in this watershed are similar to those in the Great Lakes. Lake Algonquin did not inundate areas of the park above 381 m, so lakes above this elevation do not share this invertebrate fauna. Several fish species followed the receding glaciers across the park landscape as the ice retreated northward and new rivers formed from the melt water (Ridgway et al. 2017). These species (e.g., brook trout, lake whitefish) occupy many areas in the park. Other fish species (e.g., cisco, trout perch) entered the park landscape via the Lake Algonquin drainage and are distributed in the northern half of the park (Ridgway et al. 2017).

Native fish species and their food webs are protected in the park aquatic network because of the Algonquin Dome — a relatively high elevation area in southcentral Ontario from which several rivers run off to the Great Lakes and the Ottawa River. Waterfalls and other barriers near the park boundary protect the native aquatic fauna from species moving upstream from outside the park's boundary (Ridgway et al. 2018a). This level of natural protection is important for several fish species and aquatic food webs unique to Algonquin Park.

Climate warming is occurring and projected to continue until mid- to late century, depending on carbon dioxide emissions (Ridgway et al. 2018b). Warming of lakes, rivers, and shallow ground water will follow the warming trend and may threaten coldwater fishes such as brook trout and lake trout. If warming continues, effects to aquatic systems will be more widespread.

Finally, for over a century, several fish species have been stocked in Algonquin Park lakes for anglers (Mitchell et al. 2017). Some were native species, such as brook trout and lake trout, while others, such as smallmouth bass, had limited native distribution in the park. By mid-20th century, the basis for stocking shifted from an initial effort to supply fish for lodge visitors to stocking that supported more intensive interior trips. Now stocking is generally limited to the Highway 60 corridor in lakes without self-sustaining brook trout or lake trout. In recent decades, species such as northern pike and rainbow smelt have been introduced illegally.

Planning is ranked as the highest management priority for parks globally (Dudley et al. 2018). Protecting aquatic values and managing fisheries has been a theme throughout the history of Algonquin Park. Because aquatic ecosystems differ from their terrestrial counterparts, considerations for conservation planning in aquatic ecosystems also differ. The first requirement in Algonquin Park is to understand the distribution of freshwater ecosystems.

Ecological integrity of freshwater ecosystems in Algonquin Park

The Provincial Parks and Conservation Reserves Act, 2006 describes an important principle guiding the planning and management of Ontario's provincial parks as "maintenance of ecological integrity shall be the first priority and the restoration of ecological integrity shall be considered." Ecological integrity, as defined in the act, "refers to a condition in which biotic and abiotic components of ecosystems and the composition and abundance of native species and biological communities are characteristic of their natural regions and rates of change and ecosystem processes are unimpeded."

The concept of ecological integrity began with the 1972 United States Water Pollution Control Act (otherwise known as the Clean Water Act) and has been associated with freshwater ecosystems since (Kuehne et al. 2017). The purpose of the act was to mandate the restoration and maintenance of the chemical, physical, and biological integrity of U.S. waters. The abiotic and biotic components of freshwater ecosystems function together, so seeking to maintain all components was a way to ensure continued ecological integrity.

Assessment and monitoring are needed to assess whether ecological integrity is maintained or changing. Ecological integrity-based assessment methods require 1) the use of a reference method that allows any site or watershed condition to be evaluated against a standard state (Chu et al. 2018) or 2) the use of methods that partition natural variability from human effects in aquatic ecosystems (Kuehne et al. 2017). Because Algonquin Park retains many aspects of its natural state in the aquatic network, several approaches, including introduction of non-native species or loss of ecosystem function, can be compared to regions retaining their natural state as a standard for ecological integrity in the park and relative to other protected or non-protected landscapes.

Kuehne et al. (2017) recommended several steps to improve assessments of ecological integrity in freshwater ecosystems. Steps relevant for conservation policy and management are:

1) **Include policy relevance in assessments.** Ensuring that monitoring efforts reflect the priorities of resource management agencies will help ensure implementation and reporting.
2) **From the start, consider management questions to inform assessments.** This eliminates a range of assessment indicators used in the past that were informative with respect to decisions about the application of ecological integrity but not relevant to management.
3) **Use methods that cleanly separate indicators** (responses to loss of ecological integrity) **from stressors** (factors that cause loss of ecological integrity). Doing so will better address policy and management concerns and lead to different monitoring and assessment approaches. For example, tracking the distribution of non-native fish through Algonquin Park watersheds directly monitors a stressor vs. trying to discern any complex food web interaction that stems from this kind of introduction in each lake.
4) **Collaborate among groups** interested in ecological integrity to inform assessment and monitoring and ensure more widely applied results. Collaboration can be helpful to distinguish between status vs. trend approaches in assessing ecological integrity resulting from different methods of collecting and using information. Determining the state of aquatic ecosystems at various geographic scales in Algonquin Park may require different monitoring methods than determining trends through time in different areas in the park.

Freshwater ecosystems of Algonquin Park

Devoid of trees and soil, the topographic elevation map in Figure 1 reveals the park to be an outcome of 1) ancient processes shaping the Canadian Shield landscape hundreds of millions of years ago and 2) glacial flow thousands of years ago that set the streams, rivers, and lakes that are in place today. The combination produced the topography and aquatic network of the park.

On the western boundary, glacial flow off the Algonquin Dome was direct and towards Lake Huron. In the north, the drainage system of glacial Lake Algonquin is clear — flowing left to right in Figure 1 in what is now the Petawawa River. During the glacial era, water from Lake Algonquin flowed eastward forming a delta system (visible in the northeast corner of Figure 1). Water discharge entered a relatively flat landscape where it drained to the Champlain Sea. Several smaller watersheds flowed to this major drainage from the north and south. In the southeast, the Madawaska River flows away from the park.

The aquatic network of Algonquin Park formed during the long process of landscape formation. In the early years after glacial retreat the lakes and rivers comprising this network likely differed from what we see today. Patterns of water discharge thousands of years ago would have reflected the depressed elevation from the weight of glacial ice and corresponding watershed connectivity. Today, after thousands of years of landscape rebound, connectivity reflects a higher elevation (by about 200 m).

The lakes, rivers, streams, and wetlands comprising the aquatic network represent the full extent of aquatic Algonquin Park. All stream orders and lakes or ponds larger than 1 ha are shown in Figure 2.

The park has 3214 lakes larger than 1 ha (Middel et al. 2019). Lakes less than 5 ha in surface area comprise 60.5% of this total (count = 1946 lakes). If lakes between 5 and 10 ha are included in the small lake category (count = 466 lakes), small lakes comprise 75% of all lakes in Algonquin Park. Most of the park’s 845 headwater lakes are in the small lake category (Ridgway et al. 2018a). The total surface area of all lakes ≥5 ha is 71,489 ha.

The river and stream network connecting lakes and watersheds is 7300 km in total length (Ridgway et al. 2018a). First order streams are where surface water flow begins in watersheds and represent 49% of total stream and river length (first order stream total length = 3600 km).

Wetland sites include distinct locations interpreted from aerial imagery such as fens, bog lakes, and lakes with extensive vegetation cover. The park has about 16,000 wetlands covering 362 km^2 (Ridgway et al. 2017).

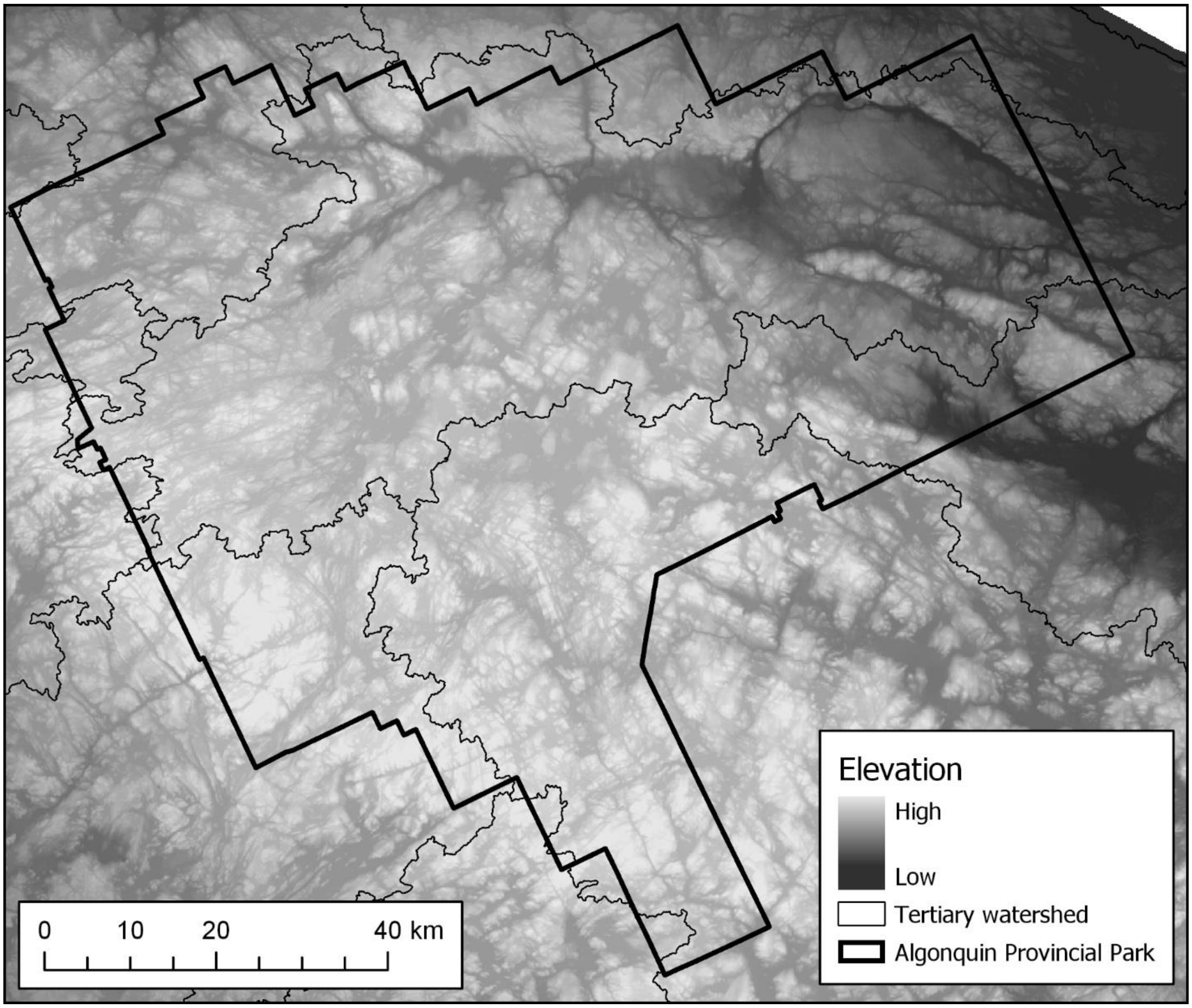

Figure 1. The topography of Algonquin Provincial Park, Ontario (boundary indicated by thick black line), and surrounding landscape. Light grey represents high elevation and dark grey or black represents lower elevation.

A separate element of the aquatic ecosystem in Algonquin Park is the shallow groundwater flow network that feeds streams, rivers, and lakes. This network is based on slope and watershed boundaries. Because the park is largely Canadian Shield rock, the topography is a good approximation of shallow ground water flow stemming from precipitation (Borwick et al. 2006). Shallow groundwater collects in small valley systems that join and eventually flow to lakes, streams, and rivers. This habitat feature is essential for brook trout spawning success and young brook trout habitat (Blanchfield and Ridgway 1997, Biro 1998, Borwick et al. 2006). The shallow groundwater seepage patterns are not shown in Figure 2.

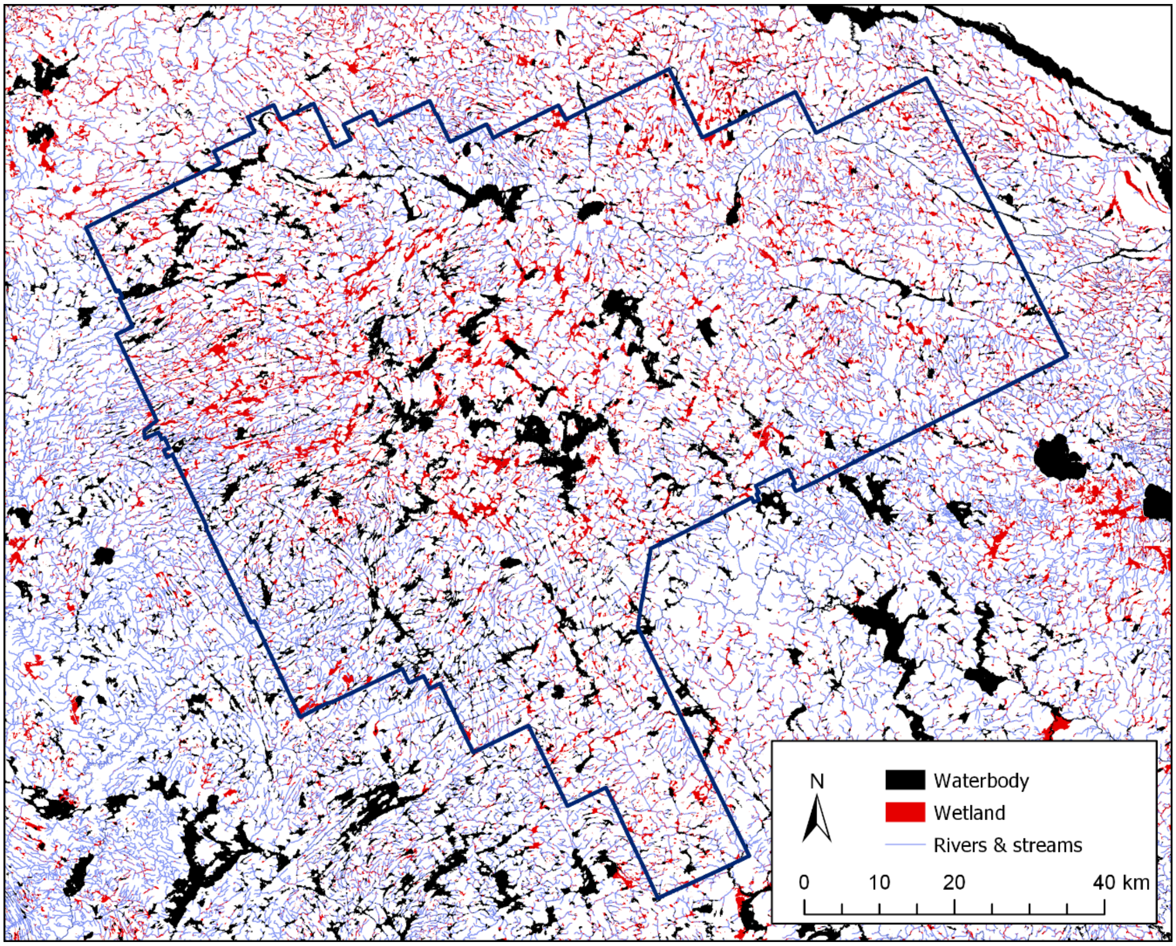

Figure 2. Lakes, rivers, streams, and wetlands of Algonquin Provincial Park, Ontario ((boundary indicated by blue line), and the surrounding landscape, illustrating the aquatic network of surface waters in the park.

Table 1 summarizes the watershed features of Algonquin Park. The nested and directional network structure associated with watersheds are key features distinguishing aquatic conservation from traditional conservation planning. The most important feature is the directional nested network of watersheds on the park landscape, especially the source water areas of the Algonquin Dome. This feature forms a natural level of protection well within the park boundaries.

Together, the extensive aquatic network is an important element of the ecological integrity of Algonquin Park. Most of the network has a low level of non-native fish species. For native fish species, the park is one of the last significant landscape areas in southcentral Ontario retaining native aquatic food webs in lakes and rivers. Aquatic conservation planning can help us to sustain this area.

Table 1. Watershed features of Algonquin Provincial Park lake, stream, and river ecosystems. Adapted from Melles et al. (2012, 2014).

Component	Description
Directional	• Flow goes one direction — lower reaches contain water representing combined flow of separate primary streams • Events in headwater systems can affect downstream ecology • River cannot be divided into different headwater streams
Nested	• Watershed begins as network of primary or first order streams that eventually grows to higher order streams as smaller sub-watersheds join • Higher order rivers cannot exist without starting in multiple locations as primary streams
Network	• Typically, is a complex of lakes, rivers, and wetlands (not a singular river system) • Watershed position is important; contributing area to any stream in watershed increases as position shifts downstream • Greater areas of watershed become linked as flow moves from primary to higher order streams and rivers • Lakes, wetlands, and confluences among streams and rivers all contribute to stream network variation
Ecosystem	• Biological community of interacting organisms and their physical environment • As aquatic ecosystems, watersheds/streams have directional flow, are nested within the watershed boundaries, and are organized as a network (small streams join to make larger ones) • Patterns in faunal zonation and primary production depend on location — structure based on directional, nested network

Elements of aquatic biodiversity conservation

At global scale, freshwater ecosystems are the most at-risk ecosystem category (Dudgeon et al. 2006, Collen et al. 2014.). The features of watersheds described in the previous section are also the elements that place freshwater ecosystems at the top of conservation concerns. Watersheds concentrate the effects of land use practices through flow into streams, rivers, and lakes that in turn carry effects over large distances downstream to other parts of watersheds. Rivers and streams provide a corridor for native and non-native species to move to other locations in the network and through confluences to other networks, often with unintended consequences.

Many rivers and streams have been partitioned through dams and diversions for human use. Dams prevent natural movement of fish. Ecosystem function can change in rivers and streams where freshwater species are overexploited or lost (Vaughn 2010). Historically, watersheds and their rivers and lakes also serve as political boundaries that can lead to complexity in use and mediation of any effects. Together, when combined with human needs for consumption and cultural importance, the priority of conserving freshwater as an ecosystem along with its biodiversity is globally important (Carpenter et al. 2011). Table 2 summarizes stressors (threat categories) affecting freshwater fish.

Biodiversity in freshwater, as represented by species richness, is more threatened than in terrestrial systems (Dudgeon et al. 2006). At global scale, several groups of aquatic species are under threat as described by the International Union for Conservation of Nature (IUCN) Red List Categories and Criteria. Of the 630 fish species listed by the IUCN, about 25% of species are at risk of extinction (range 16–40%; Collen et al. 2014). Threat of extinction is higher for IUCN listed amphibians (about 35%; range 24–45%) and crayfish (about 30%; range 20–50%) (Collen et al. 2014). When IUCN listed species are aggregated into their habitats as lakes, marshes, or flowing waters, the threat of extinction is highest for flowing waters at about 35% (range 22–55%; Collen et al. 2014). Lakes and marshes have similar extinction/ threats for aquatic species at about 20 to 22% of listed species.

The scale of this global threat is reflected in North America. About 39% of the fish fauna in North America is imperiled, meaning species fall somewhere on the ranking system of endangered, threatened, vulnerable, or extinct (Jelks et al. 2008). This represents a jump of 92% in imperiled fish species over a 20-year period. This upward trend in fish population declines and species in peril continues (Reid et al. 2019). Habitat degradation and effects stemming from introduced species are the main threats affecting imperiled fish and freshwater ecosystems (Jelks et al. 2008; Reid et al. 2019).

In Canada, tertiary watersheds in the southern regions of British Columbia, Ontario, and

Table 2. Stressors, or threat categories, affecting freshwater fish biodiversity (from Chu et al. 2003, 2015; Dudgeon et al. 2006; Jelks et al. 2008; Sharma et al. 2009; Olden et al. 2010).

Threat category	Examples
Water pollution	Point-source additions of chemicals; landscape runoff from agriculture and urban centres; downstream accumulation of chemicals
Overexploitation	Harvesting fish beyond sustainable limits of production
Habitat degradation	Loss of nearshore habitat such as riparian zones; substrate siltation; removal of aquatic macrophytes and shoreline structure; land use practices changing hydrology and runoff
Flow modification	Dams blocking natural flow regimes; water diversion from rivers and streams affecting total volume; channelization
Species introductions	Authorized or non-authorized introductions of species not native to watershed; introductions of exotic species from elsewhere in the world; introduced predators consuming local species; introduced prey species competing with native species
Climate change	Changing temperature regime leading to changing water conditions; effects on spawning timing; effects on physiological tolerances; loss of appropriate thermal habitat for fish

Quebec have high conservation priority rankings based on fish species and the presence of relatively rare species (Chu et al. 2003). All tertiary watersheds in Algonquin Park (and southcentral Ontario) are ranked as a high to critical conservation priority at national scale based on species conservation rankings, environmental indices (growing degree days, topographic relief, and warmth), and high stress based on human population density and land-use patterns (Chu et al. 2003). A similar conclusion was reached for the Algonquin Park region of southern Ontario based on the extent of human land use and fragmentation, water quality decline, and species introductions (Abell et al. 2000). In more recent updates (Chu et al. 2015), all tertiary watersheds in Algonquin Park and southern Ontario are ranked as a high to critical conservation priority for fish species at national scale. This status has remained unchanged in recent decades (Chu et al. 2015).

What would account for this high conservation priority ranking since about half of Algonquin Park is within protection zones of various types? No single tertiary watershed is fully contained within the boundaries of Algonquin Park. Areas of each watershed extending beyond park boundaries enter a region of relatively high human stress stemming from land use and population density that characterizes much of southern Ontario. While Algonquin Park itself is not subject to most stresses that affect landscapes adjacent to it, and more broadly across southern Ontario, the high to critical ranking for its tertiary watersheds is a reminder of the importance of the park for aquatic conservation in the larger landscape. The park has relatively high ecological integrity compared to areas outside it, even in the same watersheds. Based on these assessments in Canada and elsewhere, a consensus has developed on the categories of threats to fish biodiversity (Table 2). Two important stressors on Algonquin Park's aquatic ecosystems are species introductions that alter natural food webs and climate warming that affects thermal conditions of lakes, streams, rivers, and wetlands.

Stressor 1. Species introductions

The use and possession of live baitfish and the overland transport of live fishes are illegal in Algonquin Park. Even so, fishes have been introduced to the park landscape. The effects of fish introductions to the park requires consideration of:

1) the stages of species introduction
2) fish movement stemming from introductions
3) bait and the risk of its introduction
4) the concept of the homogenization of fish fauna resulting from introductions

Aquatic species introductions or invasions occur at much finer scales than are evident at the scale of tertiary watersheds. Individual lakes or streams can be sites of introduction followed by a sequence of steps that can lead to an established population of the introduced species and subsequent vulnerability of native species. Both population status and vulnerability status are based on the same stages of introduction but assessment questions about the effects of introduction differ (Table 3). For population status, questions focus on population ecology of the introduced fish as its numbers change from relatively few at the time of introduction to reaching carrying capacity of a lake's environment. For vulnerability status, questions focus on features limiting access to or occupancy of lakes such as the road network, aquatic connectivity, or lake habitat features that may or may not be suitable for some species.

When fish species are introduced to a new watershed or lake ecosystem the founding population follows a trajectory through several stages of introduction. The trajectory can be divided into four phases: 1) arrival, 2) establishment, 3) expansion, and 4) capacity (Table 3). Effects of the arrival of introduced fish species may include displacement of native species from prominence in aquatic food webs, extirpation of native species and especially small-bodied fish species due to predation, or disruption of production pathways leading to changes in the size and abundance of fish such as lake trout and brook trout.

Table 3. The stages of fish introduction and whether population status or lake vulnerability is the focus of assessment. Both kinds of status associated with the stages of introduction are relevant for assessing fish introductions in Algonquin Park. (Modified from Shuter and Ridgway 2002, Vander Zanden et al. 2004, and Vander Zanden and Olden 2008.)

Stage of introduction	Lake population status	Lake vulnerability status
Arrive	Are individual fish introduced to a lake?	Can an introduced species get to a lake or a set of lakes?
Establish	Are there enough individuals to start a breeding population? Will the population grow?	Which lakes will support a self-sustaining population?
Expand	Can the population expand to fill the lake spatially and by numbers? Will the population occupy the lake?	Will an established introduction reduce the native species present and alter the food web? Will it have an effect?
Capacity	What is the carrying capacity for the introduced species? What drivers are causing population fluctuation?	Will the introduced species spread to other lakes, repeat the introduction stages, and become established in new locations?

Population growth is initially slow as the invading species becomes established in the new ecosystem. Slow population growth could stem from too few breeding adults available to establish a breeding population. The numbers of fish in the introduction, referred to as propagule pressure, may or may not accelerate the arrival and expansion phase. Once established, a species invader enters the expansion phase of their population trajectory, which can be defined as expansion in numbers of individuals as well as geographic distribution. In the expansion phase, the population grows to it's carrying capacity or beyond in the receiving watershed or lake. The limits of expansion could be defined by factors such as ecosystem productivity and the availability of appropriate habitat. Following the expansion phase, an introduced population is said to be in the capacity phase. This phase generally results in fluctuations in population abundance as the species settles into the natural limits of ecosystem productivity including the food web where predators and prey help define carrying capacity.

The occurrence of smallmouth bass in Lake Opeongo is a case study in the changes in population status based on the stages of species introduction (Shuter and Ridgway 2002). Initially, over two decades, abundance was low, and growth of individual bass was high reflecting the low density. Growth was particularly high for juvenile bass but declined sharply in the expansion phase after about 17 years in the establishment phase. The decline in growth occurred because smallmouth bass density in Lake Opeongo increased (Shuter and Ridgway 2002). The expansion phase lasted for about 21 years during which the declining size of juvenile bass translated into smaller adult fish. In the capacity phase, the negative relationship between growth of young-of-year smallmouth Bass and abundance intensified – resulting in decreased survival in the first year of a cohort. The sequence of moving from establishment in the beginning of the Lake Opeongo smallmouth bass population a century ago to the capacity phase in recent years represents changes in bass population regulation. Density-dependent effects shifted from juvenile abundance initially (establishment), to adult abundance (expansion), and finally to young-of-year abundance (capacity).

Rainbow smelt were detected in 2009 in the diet of lake trout in Tim Lake, on the western boundary of Algonquin Park. In 2011, schooling rainbow smelt were detected during hydroacoustic surveys along the north shore of Rosebary Lake downstream of Tim Lake. In 2016, a single rainbow smelt was detected in Catfish Lake, many kilometres downstream from Rosebary Lake in the same watershed. It is unclear how many years it will take for the smelt population in downstream lakes to move from the establishment to the expansion and capacity phases of their invasion trajectory. For lakes on the Tim River system and downstream, rainbow smelt may be in the expansion stage in Tim Lake since they are part of the lake trout food web, in the establishment stage in Rosebary Lake based on the detection of a school of fish, and in the arrival stage in Catfish Lake based on the detection of a single rainbow smelt. Perhaps none of the lakes are yet in the capacity stage but dominance of smelt in the lake trout diet would confirm this possibility.

Rainbow smelt are achieving all four stages with respect to vulnerability status of lakes on the Tim River and downstream in lakes of the Upper Petawawa River. They are now found in several lakes (Tim, Rosebary, and Catfish) and passed through several more (Longer, Burntroot) but have yet to be detected in these lakes (arrival stage). In Tim and Rosebary Lake, which are relatively small, the numbers of smelt are growing or have established new populations (establishment stage). Tim Lake appears to be the only one with a large enough population to be included in the diet of lake trout (expansion stage). Finally, the set of lakes downstream in the Petawawa River could be occupied by rainbow smelt since they've become established in relatively small lakes (capacity stage).

Two general approaches have been used to examine factors determining lake occupancy by different fish species at finer scales below a national comparison of tertiary watersheds. One approach examines the influence of a set of parameters such as lake characteristics (e.g., surface area, depth, elevation), climate (e.g., average temperature), and species characteristics of the fish assemblage (e.g., prey size, fish assemblage, thermal niche) to determine if these variables serve as a filter that can account for the presence or absence of fish in lakes. This approach relies on a set of parameters thought to filter species occurrence based on factors such as habitat preference, physiological tolerances for temperature, or degree of isolation in the landscape. In the absence of the preferred environment, a fish species cannot become established. One good example of this approach is the absolute requirement for deep cold water in summer months for cold adapted species such as lake trout, lake whitefish, and burbot. Without cold water during summer months these species cannot persist in lakes.

The other approach examines aquatic connectivity to determine if fish species occupy lakes in a landscape based on access, sometimes regardless of environmental parameters. This approach can rely on connectivity alone if lake environments are relatively similar across the connected network. Connectivity may be enough to account for species presence or absence because lakes within regions tend to be similar with respect to environmental parameters. Within the network, lakes may be generally suitable or not based on whether they provide some minimum level of suitability as in the case outlined above for coldwater fish.

An implicit assumption in the natural filtering approach is that lakes are accessible, and the environment asserts control over presence or absence of a species. A comparison of lake occupancy by lake trout and smallmouth bass in the southcentral Ontario landscape from the Algoma region through Algonquin Park and eastern Ontario was based on a filtering approach to assess co-occurrence of the two species (Vander Zanden et al. 2004). Smallmouth bass occurrence could be separated from that of lake trout across much of the landscape using glacial history as a measure of initial fish occupancy in lakes. This is because lake trout initially occupied lakes after deglaciation and smallmouth bass were absent because early lake environments were too cold for them. The late arrival of smallmouth bass to watersheds long after ice retreat thousands of years ago points to their warm water preference (Ridgway et al. 2017). Similarly, large lakes in more northerly locations (lower mean air temperature) with several established piscivores were less likely to have smallmouth bass since glaciation (Vander Zanden et al. 2004). The natural filtering approach to understanding fish distribution in Ontario requires knowledge of stocking history to account for current distributions.

A closer inspection of smallmouth bass occurrence in southcentral Ontario indicates that a combination of natural dispersal following deglaciation as well as stocking history underlies their occurrence (Vander Zanden et al. 2004). Lack of smallmouth bass in Algoma region lakes and inland lakes north of Lake Huron reflects glacial history and limited access based on occurrence data from the 1970s. For this reason, many lakes were ranked as low vulnerability for bass access and spread. Unauthorized stocking in this region has resulted in widespread distribution of smallmouth bass in many lakes of southcentral Ontario that are also occupied by lake trout. Smallmouth bass was predicted to occur in many Algonquin Park lakes but has yet to reach them because of park regulations and limited access. Similarly, many lakes in the Highway 60 corridor were predicted to not have smallmouth bass but do because of stocking early in the

20th century. Finally, smallmouth bass was predicted to be absent from Lake Travers — the only lake in the park with a historical record of having had a native population (Dymond 1936, Ridgway et al. 2017).

What can be concluded from this filtering approach? First, and most importantly, the distribution of fish following the period of glacial retreat across many landscapes of Ontario does reflect natural protection from introductions because of natural barriers to movement in and among watersheds. Second, this pattern of historical presence or absence of fish can be easily disrupted by species introductions and subsequent spread. Third, road access or other modes of access have shifted the arrival component of vulnerability status from what was thought to be low based on post-glacial distribution of fish to high. Because most lakes in southcentral Ontario can support smallmouth bass given their wide environmental tolerances, and the widespread introductions of predator and prey fish in Ontario over the past century the final lesson is that, when assessing vulnerability, aquatic connectivity is an essential consideration.

Aquatic connectivity

The key to a deeper understanding of where introduced fish species can occur is aquatic connectivity among watersheds along with physiological and species-specific habitat requirements (Spens et al. 2007, Vander Zanden and Olden 2008). Connectivity can be as simple as the slope of connected stream systems where slope thresholds define the limits of spread, as in the case of northern pike (Spens et al. 2007). In other cases, landscape features such as watershed area, stream gradient, landscape slope, and barriers combine to prevent inland movement of invasive species such as round goby from the Great Lakes to inland locations (Kornis and Vander Zanden 2010). In both examples, features of watersheds and streams were enough to map the distribution of introduced fish without solely relying on an environmental filtering approach.

When accounting for species distributions in Algonquin Park, environmental and spatial variables can be relevant as can the presence of introduced predatory fish. Introduced predators do lead to the extirpation of small bodied fish species and alter the distribution of other species in the park (MacRae and Jackson 2001, Trumpickas et al. 2011). Non-native predatory fish species are distributed from where they were introduced, with subsequent spread through a watershed based on aquatic connectivity (Trumpickas et al. 2011). Introduced predators like smallmouth bass greatly reduce small native fish species in Algonquin Park lakes; however, increasing the number of introduced predatory fish species does not result in corresponding increases in loss of species richness (Trumpickas et al. 2011). Variation in patterns of fish assemblage structure — differences and similarities of the compliment of fish species in lakes and rivers — can be accounted for by the presence of an introduced predator, but the greatest variation in assemblage structure among lakes can be accounted for by lake location, size, elevation, and environmental parameters. This is a filtering effect at smaller scales closer to the scale of where fish occur and do not occur in a watershed. The importance of spatial variables also points to watershed processes such as glacial history and aquatic connectivity for insight into species distribution. This aquatic history of the park landscape explains much of the distribution.

Aquatic connectivity is a fundamental element for the ecology and conservation of stream fish. Connectivity facilitates functional links for fish that use streams and rivers for most of their life history. Zonation of fish in rivers, or how fish species and assemblages fall into repeatable patterns of occurrence along the lengths of rivers, requires some degree of connectivity to support different life stages of fish. Movement among stream or river segments, and their associated habitats, fulfills seasonal habitat requirements for different life history stages (Schlosser 1991, Fausch et al. 2002, Wiens 2002).

Fish movement

The mapping of watershed boundaries and aquatic connectivity in Algonquin Park implies fish move extensively and perhaps completely cover the full distance of a given watershed, depending on barriers. This may be the case for some individual fish or even species, but movement within a season over the full distance of a watershed is unlikely. Generally, fish movement in rivers and streams, and therefore connectivity among lakes, is of two kinds. In the first category, long distance movements outlining the full extent of travel are typically associated with seasonal events such as spawning or taking up residency in over-winter sites or summer home ranges. Smallmouth bass have been recorded travelling 70 km between summer and winter locations (Langhurst and Schoenike 1990). Northern pike have been observed to move 16 to 240 km over 18 to 75 days, respectively (Spens et al. 2007). Departure of brook trout from lakes to downstream habitat occurs almost entirely in spring (Josephson and Youngs 1996).

The other category of stream and river movement occurs more regularly and comprises two scales of movement within seasons. Many fish disperse relatively small distances in streams and rivers and appear rather stationary. Others in the same population are more mobile and travel greater distances. The distances covered are related to fish size, stream order, and fish body design, with those designed for swift movement covering greater distances than those designed for life on the bottom of streams and rivers (Skalski and Gilliam 2000, Radinger and Wolter 2014).

The stationary vs. mobile contrast is also observed in lake dwelling fish. Brook trout in Mykiss Lake have the same stationary/mobile pattern in each cohort of young brook trout that emerge from spawning areas in lakes and then proceed to disperse around the perimeter of the lake in the shallow zone (Coombs and Rodriquez 2007). Most brook trout young-of-year move relatively short distances and remain near the spawning area after emergence from gravel beds. Fewer brook trout young-of-year move quickly around the lake perimeter (Coombs and Rodriguez 2007).

Generally, fish dispersal in watersheds has two scales of movement (seasonal vs. within season) and multiple time scales (days, weeks, months) over which movement occurs (Table 4). First, over relatively brief periods, large-scale movement through watersheds occurs in the shoulder seasons — spring and fall — when fish may be on spawning runs or seeking new locations for winter survival. Second, over relatively longer periods, smaller scale movements occur as either stationary or mobile components of a population but rarely match the seasonal large-scale movements. Therefore, aquatic connectivity among lakes in Algonquin Park ought to be facilitated by large-scale movements at restricted times of the year (spring and fall) and smaller scale movements during other times of the year (stationary and mobile individuals).

Table 4. Fish movement can be broadly partitioned into categories based on season, timing, and extent, with each category contributing to fish dispersion in watersheds.

Movement type	Timing	Duration	Example
Seasonal	Shoulder seasons; spring and fall	days and weeks	Annual movements to spawning habitat or overwintering habitat
Within season: stationary	In any season	days, weeks, and months	Holding feeding territories
Within season: mobile	In any season	days, weeks, and months	Movements within home range or to find new home range

Bait and risk of introduction

Live bait use is illegal in Algonquin Park. This restriction is because any transport and illegal dumping of unused live bait (and the water it's held in) is a potential pathway for introductions of aquatic invasive species that can disrupt native lake food webs and risk the genetic integrity of park fish populations. Like most anglers, those using live bait travel long distances to fish in lakes across Ontario. Results of Ontario-based social surveys and transportation models point to very low but persistent risk of introduction of non-native species (e.g., round goby; Drake and Mandrak 2014) through the bait pathway. Algonquin Park has limited public road access and is mostly outside the transportation network that serves as corridors for bait movement by anglers during the open water season. In areas of tertiary watersheds that are outside park boundaries but originate in the park, the risk of introductions from dumping of bait buckets is real, and this risk essentially surrounds the park (Drake and Mandrak 2014).

Angling trips where illegal and invasive species (e.g., round goby or rainbow smelt) are used as bait are relatively rare. Most anglers are conscious of the risk of spreading invasive species through bait bucket releases and the potential effects of these species on native fish food webs; however, roughly 30% of anglers continue to release unused bait (Drake and Mandrak 2014). Since over 4 million angler trips with live bait occur per year in Ontario, the risk is low but persistent. Based on travel destinations, models of bait use and release, and the frequency of non-baitfish species in the bait supply, regions surrounding Algonquin Park are projected to receive introductions of invasive species (e.g., round goby, rainbow smelt). The risk is referred to as *propagule pressure* meaning the seeding of ecosystems with a non-native species. The propagule pressure for round goby does not mean that an introduction will lead to the establishment phase of an invasive population, but it does indicate that the risk persists and an establishment phase is possible. Based on these factors, the potential is high that round goby or other invasive species will be introduced to high destination waterbodies surrounding Algonquin Park, including the large Muskoka Lakes (Rosseau, Joseph, and Muskoka) and the Ottawa River (Drake and Mandrak 2014).

Given the extent of fishing trips using live bait, any small risk on a per trip basis scales up to over 3,000 risky bait trips per year in Ontario (Drake and Mandrak 2014). The extent of a subset of these trips occurring in Algonquin Park is unknown. The extent of these trips to watersheds near or adjacent to the park is also unknown. Several watersheds, including the Petawawa River, originate outside the park boundary and are sites for potential introductions that can affect lakes and rivers in the park (Ridgway et al. 2018a). Given watershed connectivity, one risky bait trip into Algonquin is too many. One way to lower the risk of spread of unwanted species is continued public education on risks to native fish.

Homogenized fish fauna

The introduction and spread of non-native fish species may reduce native fish species diversity through lake-specific extirpation of resident species. Some fish species may be lost or greatly reduced by means of predation, competition, or loss of genetic diversity from mixing of different historical populations. The development of a common, non-native food web stemming from introductions leads to:

1) loss of native fish species diversity over geographic areas
2) a common landscape-scale food web pattern often at the expense of native predators as well as prey
3) irreparably altered native, long-standing fish and aquatic food webs

This process is referred to as homogenization of fish fauna (Rahel 2000, 2007, 2013). Homogenization is not simply the loss of species resulting in lower species richness but also the replacement of native predator species with predatory species from other regions or continents. Similar or identical aquatic food webs develop over large geographic regions and native species diversity declines. For the park, homogenization of the fish fauna will result in the loss of species diversity and unique populations of fish. Mitigation is difficult to impossible because it requires removal of introduced species. Several key features of this reduced diversity are described below.

In Algonquin Park, reduced species diversity often results from introduced predators causing the extirpation of small body fish species (MacRae and Jackson 2001, Trumpickas et al. 2011). Natural food webs can be disrupted because introduced predators or prey fish cause changes in native species diet as observed in lake trout populations (Vander Zanden et al. 1999). Introductions of rock bass or smallmouth bass leads to these species dominating consumption of prey fish previously available to lake trout, especially in smaller lakes where new top predators displace lake trout, decreasing their size.

Fish species distribution in lakes across the park reflects historical occurrences of post-glacial drainage from ice-age Lake Algonquin and food web differences based on the presence of a large planktonic predator, the opossum shrimp (*Mysis diluviana*). Known as *Mysis,* this plankton defines inundation by Lake Algonquin (Martin and Chapman 1965, Ridgway et al. 2017). Life history diversity among the iconic coldwater fish species of Algonquin Park is unique in Ontario and is a direct outcome of the post-glacial period and formation of the watersheds we see today.

Lake trout occur in three food web types that are based on prey composition. Small body lake trout have limited foraging opportunities where large prey fish such as cisco and lake whitefish are absent from open water. These are referred to as Type 1 lake trout populations. Type 2 lake trout lakes include cisco, lake whitefish, or both as part of the food web. Finally, Type 3 lake trout lakes include species found in Type 2 lakes as well as the opossum shrimp or *Mysis,* which is restricted to lakes in the northern regions of the park (Ridgway et al. 2017). Because of their ability to broadly affect planktonic size structure of lakes and in turn the upper levels of lake food webs, *Mysis* are considered a food web engineer. In Type 2 and 3 lakes, lake trout reach larger body sizes because of larger prey but Type 3 lakes have a longer food chain because *Mysis* generates a new level in the food web.

Lake whitefish show remarkable variation in their size and life history across the park landscape, including an exclusively open water form in Lake La Muir that is unique in North America. All these features of native coldwater fish species like lake trout, brook trout, and lake whitefish are at risk of loss if non-native predatory fish and prey fish are introduced to the watersheds of Algonquin Park. Introductions of bass to Type 1 lake trout lakes results in bass controlling inshore lake production that in turn reduces lake trout growth and size (Vander Zanden et al. 1999).

The introduction of smallmouth bass to park lakes over a century ago illustrates the process of homogenization (Mitchell et al. 2017). From a history of fish stocking and anecdotal reconstructions of their introduction, a distribution can be mapped based on known introductions and subsequent sightings in other lakes. If smallmouth bass are found in lakes connected to stocked lakes, it is likely they spread through the watershed to the lakes. If a barrier separates lakes in watersheds, the presence of bass in lakes other than those with recorded introductions points to new introductions whether authorized by park staff or not. Many of these locations were established many decades ago (Mitchell et al. 2017). This pattern of smallmouth bass stocking and spread has been repeated across the Ontario landscape and other regions, with bass introductions leading to loss of small native fish species (Whittier et al. 1997, Findlay et al. 2000, Jackson 2002).

In lakes, introduced predators can occupy important positions in the food web, often appearing to capture food resources from both the pelagic (open water zone of a lake) and littoral (nearshore zone of a lake) zones along with narrowing the food web position of native species (Sagouis et al. 2015). Homogenization of fish fauna through introductions, especially predator introductions, has profound effects on species diversity and food web function in lakes and rivers. Currently, introduced fish predators are confined to heavily used access areas of the park, often linked to historical locations of lodges in the early 20th century (Figure 3; Mitchell et al. 2017).

In Algonquin Park, several introduced sportfish and prey species contribute to the homogenization of the fish fauna (see Figure 3 for predators). The sportfish species occur in other areas of Ontario, and therefore are native to Ontario but are not native to most of the Algonquin Park landscape. For smallmouth bass, muskellunge, walleye, and rock bass only Lake Travers likely constituted their native range in the park (Dymond 1936). Their preference for warmer water resulted in their late arrival to the park landscape relative to coldwater species such as lake trout, brook trout, and lake whitefish. Three of these species found in Lake Travers

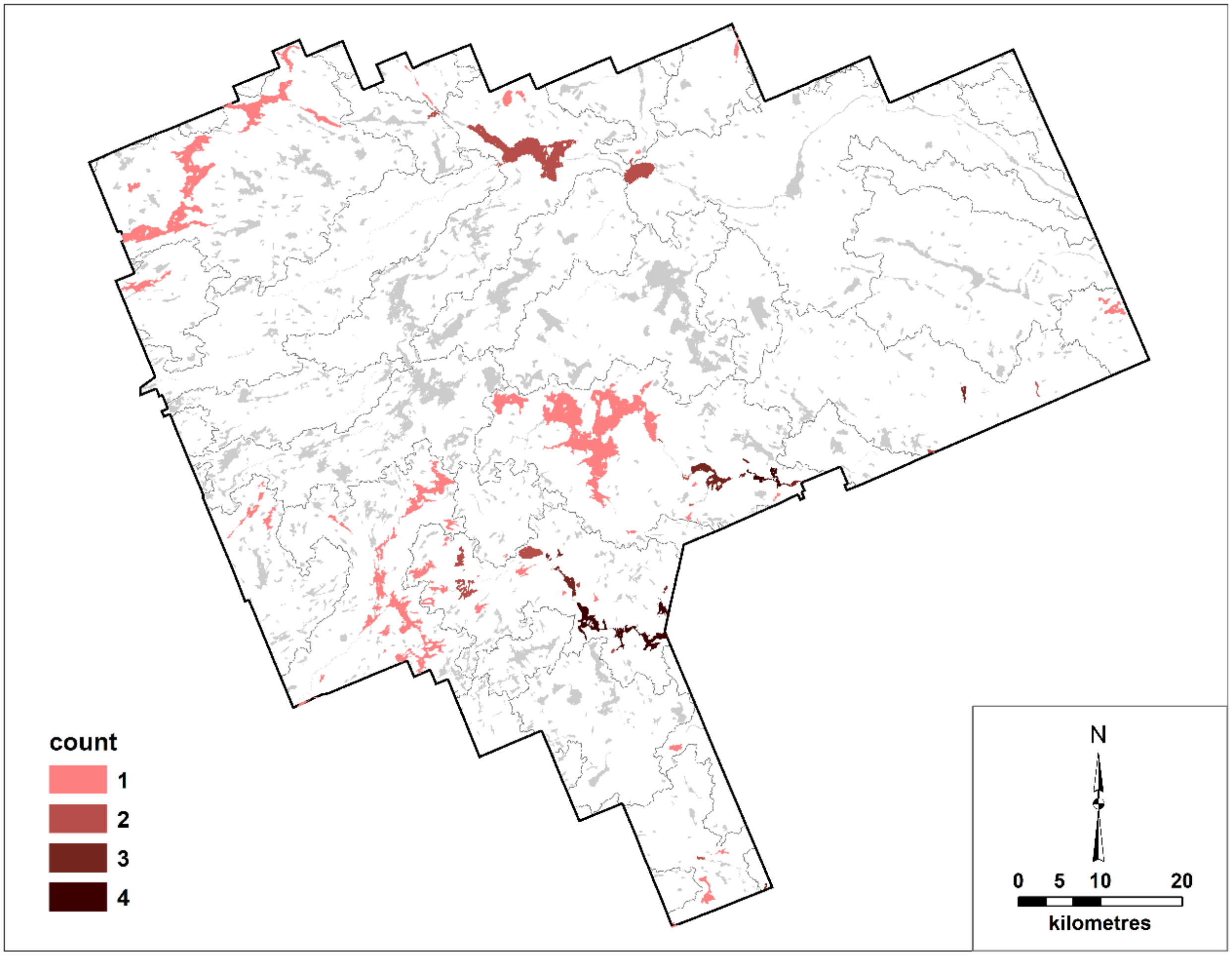

Figure 3. Number of introduced predator fish species in lakes of Algonquin Provincial Park, Ontario. Predator species that have invaded the park include non-native smallmouth bass, rock bass, largemouth bass, Arctic char, northern pike, and walleye.

(not muskellunge) have been introduced, either authorized or unauthorized, to other areas of Algonquin Park (see Figure 3). Most but not all these introductions have occurred in the Highway 60 corridor.

Barriers to movement within and among watersheds would limit the effects of introductions on native fish species. Watershed protection from fish species introductions is therefore based on the location of potential barriers that prevent access to watersheds.

Stressor 2. Climate warming in the 21st century and small lakes in Algonquin Park

The second major stressor for Algonquin Park is the warming trend caused by climate change. Later formation of lake ice, shorter durations of ice cover, and long-term increases in air temperature all point to warming (Ridgway et al. 2018b). Warming will affect the park landscape in ways that may threaten sustainability of fish and other aquatic species. The decline in ice cover duration is occurring in temperate regions worldwide (Sharma et al. 2016). Ice free winters are projected for many lakes in Ontario in this century (Sharma et al. 2019). This pattern results in longer open water seasons and points to longer periods of warm/cold water stratification.

For most lakes in the Northern Hemisphere, ice cover will be intermittent — meaning in some years lakes will have ice cover and in others not — under warming scenarios resulting in mean annual air temperatures exceeding 8.4 °C (Sharma et al. 2019). This scenario can become reality for most of Ontario if carbon emissions and corresponding warming are not reduced by mid-century (Sharma et al. 2019). Algonquin Park may fall into this category in the second half of the 21st century. Under warming scenarios without reductions in carbon emissions by mid-century (6.5 and 8.5 RCP categories; IPCC 2014), most or all park lakes will have intermittent ice because average air temperature will exceed 8.4 °C (Ridgway et al. 2018b, Sharma et al. 2019).

Under warming conditions with reduced carbon emissions by mid-century (4.5 RCP; IPCC 2014), annual lake ice cover will occur on the Algonquin Dome, but the landscape surrounding Algonquin Park will be characterized by intermittent ice by the end of the century (Ridgway et al. 2018b, Sharma et al. 2019). If the park retains winter-long ice, by the end of this century it may be the last region in southcentral Ontario to do so.

Declines in brook trout populations in Algonquin lakes are good examples of the potential effects of climate warming that we may see this century. Most brook trout lakes are less than 100 ha, with many less than 50 ha (Figure 4). Projected warming will affect these smaller lakes more than larger ones. Projected warming can affect brook trout in lakes in two ways. First, this species' upper temperature tolerance is 21 °C, after which physiological impairment begins to occur (Chadwick et al. 2015, Chadwick and McCormick 2017). Warming conditions will increase the volume of surface water above this threshold during the summer months and likely extend these conditions over longer periods. Because preferred thermal habitat for sub-adult brook trout is 13–17 °C (Smith and Ridgway 2019, Smith et al. 2020), projected warming may require sub-adults to shift their rearing habitat and occupy deeper areas of lakes. Second, adult brook trout thermal habitat is more variable and cooler in small lakes than in larger ones (Smith et al. 2020). Warming projections point to longer periods of summer lake stratification (warm water over top of cold water) that will constrain brook trout in habitats with lower dissolved oxygen and smaller volumes of preferred habitat than observed today.

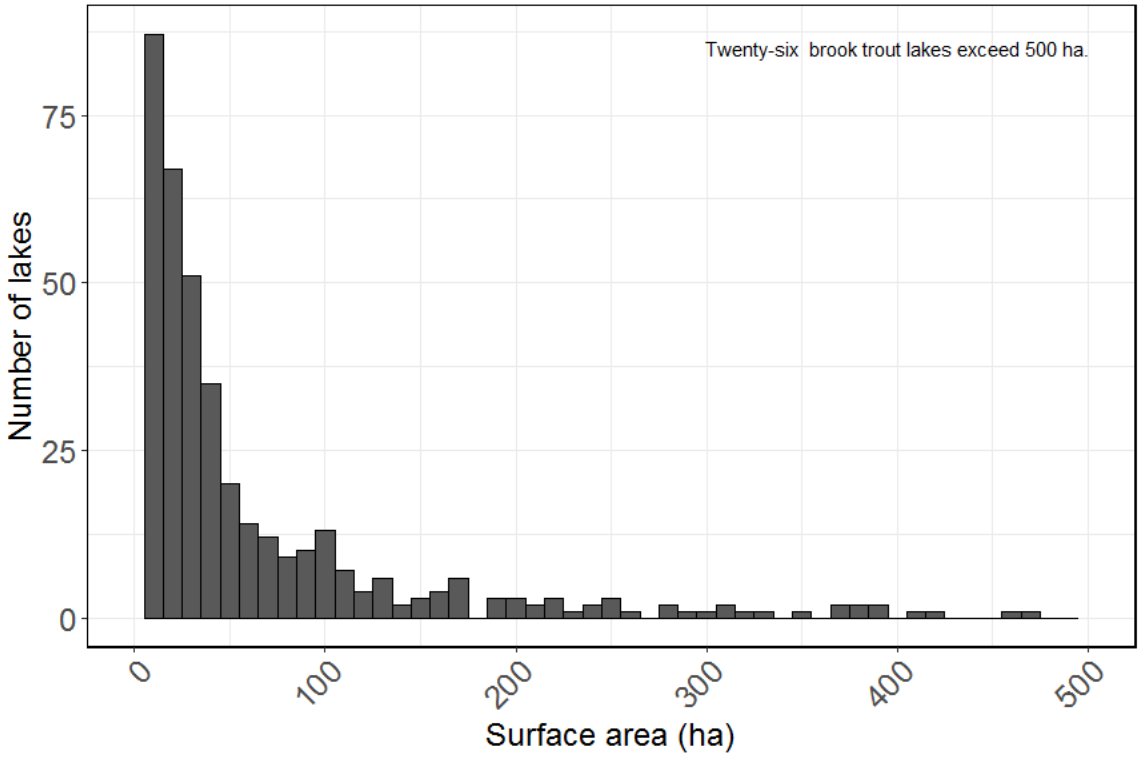

Figure 4. The distribution of brook trout lake sizes in Algonquin Provincial Park, Ontario, based on lake surface area. Most brook trout lakes are smaller than 50 ha.

Climate warming will lengthen the open water season leading to longer periods of warming summer conditions. Seasonal warming will start earlier in spring and last longer into the fall before cooling late in the year. The longer warmer season means water temperatures in lakes will increase and potentially reduce the quantity of 13–17 °C cool-water habitat preferred by brook trout.

Assessing how dissolved oxygen in water will change is more difficult. While warming reflects the physics of water, dissolved oxygen concentration reflects complex biological processes including decay of organic matter. Currently, many small lakes in Algonquin Park become anoxic below only a few metres, rendering habitat unsuitable for almost all organisms. Any decline in dissolved oxygen will exacerbate thermal habitat loss leading to further loss of brook trout habitat.

As heating extends over longer periods each year, the volume of cold water habitat in lakes may decline. Changes in future wind conditions, and therefore mixing levels in lakes, will determine the extent of these changes. Species such as lake trout, lake whitefish, and brook trout need cold water habitat to survive the warm summer season. Ground water temperatures tend to reflect average annual air temperature over the long term, so climate warming will lead to warming ground water. Because brook trout require ground water as rearing habitat for eggs and young, warming may alter spawning seasons.

Another aspect of climate warming effects on lakes in Algonquin Park has been observed in Dickson Lake where a bloom of cyanobacteria, or blue-green algae, occurred in 2014. The combined effects of long-term warming and specific ice-out and weather conditions that year combined to produce the bloom (Favot et al. 2019). Analysis of mud cores from the lake bottom of Dickson Lake is equivalent to examining a time capsule where changes in microorganisms and chemical compounds reveal a history of landscape and lake change (Favot et al. 2019). This analysis revealed changes in productivity and long-term warming.

Algonquin Park fish distribution retains the story of post-glacial recolonization

Each of the 60 species of fish native to the park entered this landscape by one of several routes following glacial retreat. The routes used by each species are evident from their current distribution in the park. Two species demonstrate this point.

The native distribution of cisco is restricted to the northern region of the park east of the abandoned lumber town of Fossmill (Figure 5). It was at this point that glacial Lake Algonquin (early Lakes Michigan and Huron) drained from west to east in what is now the Petawawa River valley. The red dotted line in Figure 5 represents the elevation limit of inundation from Lake Algonquin drainage. Cisco occupy lakes in this historical drainage as well as lakes above the elevation limit of Lake Algonquin waters because they were able to move upstream at these locations and into lakes.

Ongoing isostatic rebound of the park landscape after retreat of the glacial ice sheet resulted in elevation increasing to the south of the cisco distribution. This rebound prevented further penetration into upland areas of park watersheds by this species.

The native distribution of lake whitefish represents a different route of entry into the park landscape (Figure 6). Because this species occupies higher elevation areas in the central region of the park, as well as the drainage system of Lake Algonquin, their entry to Algonquin Park included tracing the retreat of the ice sheet and possibly drainage from Lake Algonquin as with cisco. If cisco had followed a similar route as lake whitefish, it would have been more widely dispersed in upland areas of watersheds. This comparison indicates that lake whitefish likely arrived on this landscape before cisco.

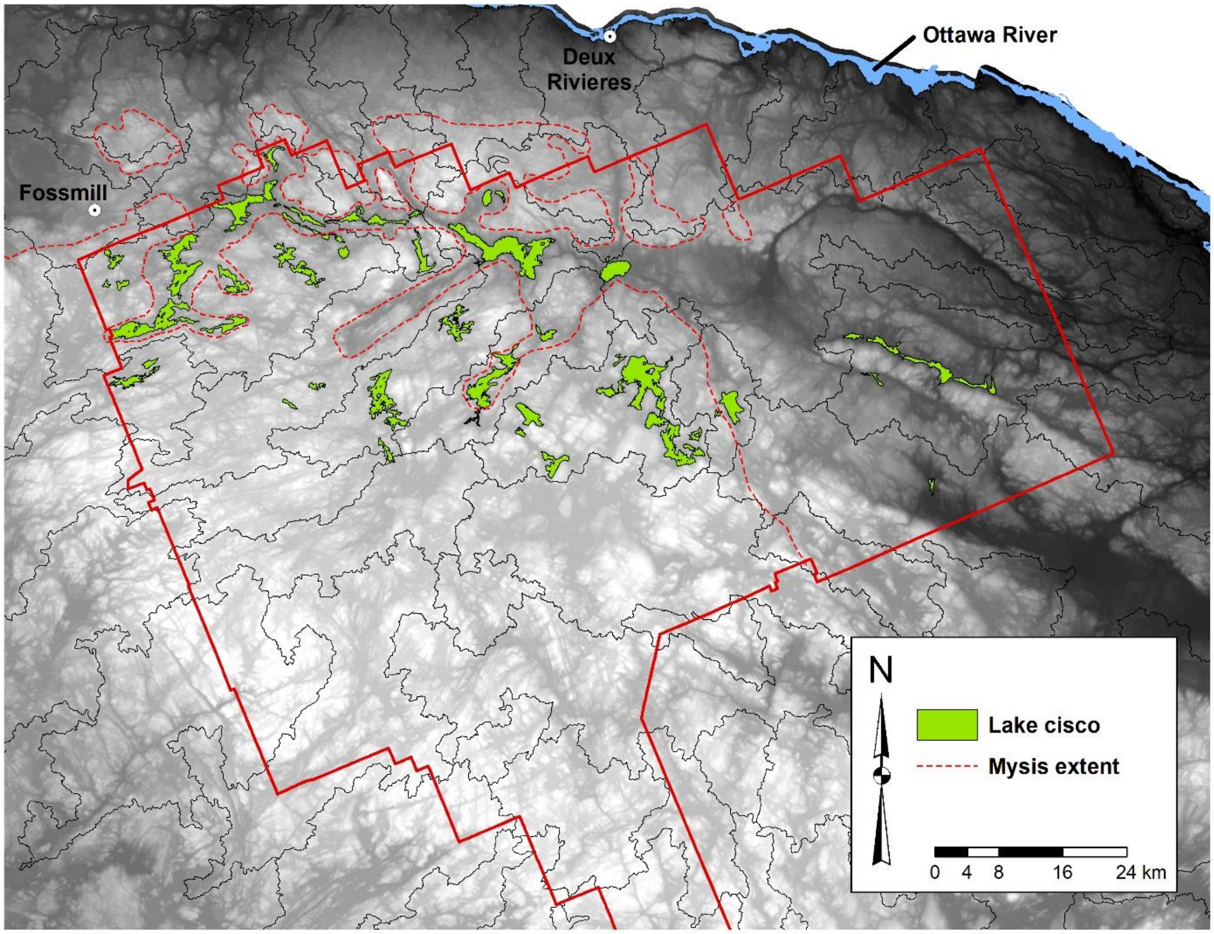

Figure 5. The native distribution of cisco in Algonquin Provincial Park, Ontario (boundary superimposed in red). The red dotted line indicates the boundary of the distribution of *Mysis* (opossum shrimp) in deep lakes in the northern region of the park. *Mysis* is an indicator of glacial inundation by drainage from Lake Algonquin 12,000 to 13,000 years ago.

Lake Travers and lower Petawawa River

Lake Travers in the northeast region of Algonquin Park has a unique story on patterns of recolonization by fish after glacial retreat. Lake Travers is the limit of distribution in the park by several warmwater fish species (Figure 7). Smallmouth bass, walleye, and muskellunge reached Lake Travers by travelling upstream in the Petawawa River from the east. They are restricted in Algonquin Park because the small waterfall on the Petawawa River at the inlet to Lake Travers prevented further upstream movement.

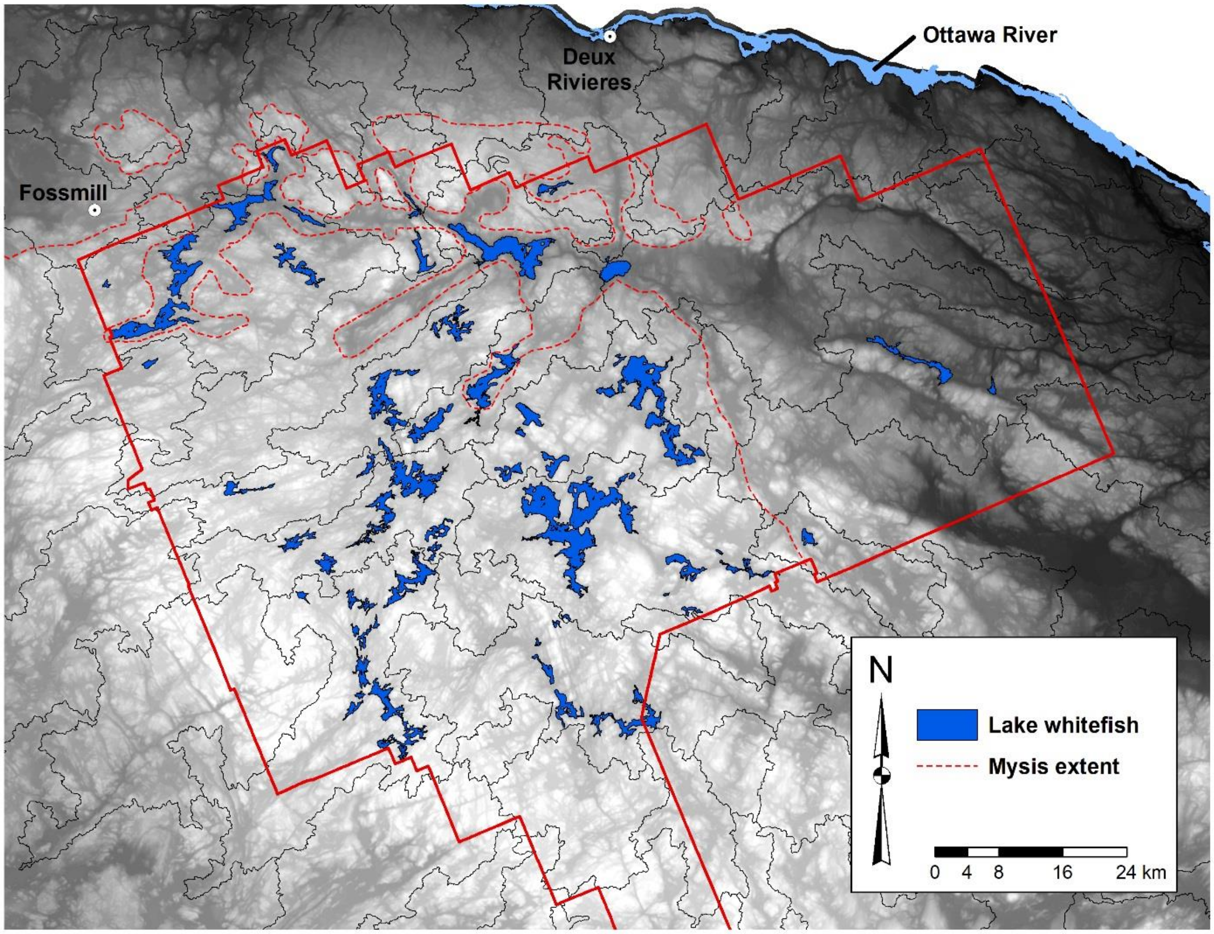

Figure 6. The native distribution of lake whitefish in Algonquin Provincial Park, Ontario (boundary superimposed in red). Lake whitefish is distributed widely, including in the Lake Algonquin drainage system and in higher elevation lakes on the Algonquin Dome. The red dotted line indicates the boundary of the distribution of *Mysis diluviana* (opossum shrimp) in deep lakes in the northern region of the park. *Mysis* is an indicator of glacial inundation by drainage from Lake Algonquin 12,000 to 13,000 years ago.

Their preference for warm water meant that tracing the movement of the retreating ice sheet or early occupancy of Lake Algonquin did not occur, as it had for cisco and lake whitefish. These warmwater species and others like them were the last to reach the park landscape after glacial retreat. By that time, the landscape had rebounded, natural barriers like water falls were in place, and their opportunity to move across the park was restricted. Since then smallmouth bass and walleye have been introduced beyond their native distribution.

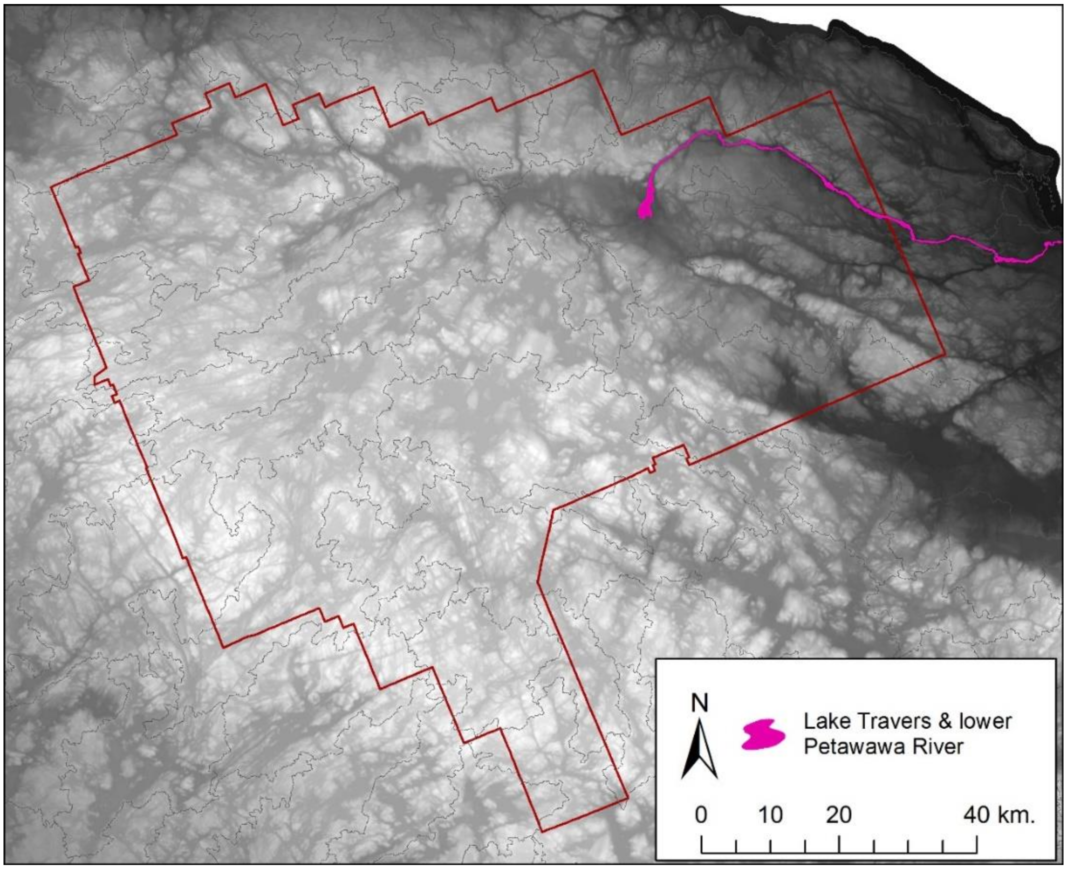

Figure 7. Lake Travers and lower Petawawa River are highlighted on a digital elevation map of Algonquin Provincial Park, Ontario (boundary superimposed in red). Smallmouth bass, walleye, and muskellunge were restricted to this area because they entered the landscape after isostatic rebound. These species are warmwater fish and would not have tolerated the cold glacial waters during the earliest stages of recolonization.

Species at risk listing for freshwater fish: Lake whitefish and cisco as case studies

The post-glacial formation of fish assemblages in Algonquin Park lakes, combined with the relative remoteness of the park have resulted in several unique populations of cisco and lake whitefish (Ridgway et al. 2017). In White Partridge and Big Trout lakes, evolved forms of cisco (Turgeon et al. 2016) and lake whitefish, respectively, have developed since post-glacial retreat. The absence of lake whitefish in White Partridge Lake and the absence of cisco in Big Trout Lake have allowed for the evolution of a unique form based on a process observed in species of the genus *Coregonus* – ecological speciation (Bernatchez 2004). Ecological speciation can be observed in species on islands, including lakes that serve as *islands of water in a sea of land*

(Schluter 1996). For White Partridge Lake, a form of cisco occupying deeper, bottom areas of the lake evolved in the absence of lake whitefish that would normally occupy that niche.

In Big Trout Lake, a form of small body lake whitefish has evolved to fill the open water niche in the absence of cisco that would normally occupy that habitat. The two lake whitefish forms in Big Trout Lake have different life histories reflecting habitat differences (Figure 8). Lake whitefish captured in bottom nets represent the form typical of most Canadian lakes with a lifespan exceeding 25 years. The pelagic form occupying the open water of the lake is smaller and similar in size to cisco — effectively a cisco mimic. Their maximum lifespan is 6 years.

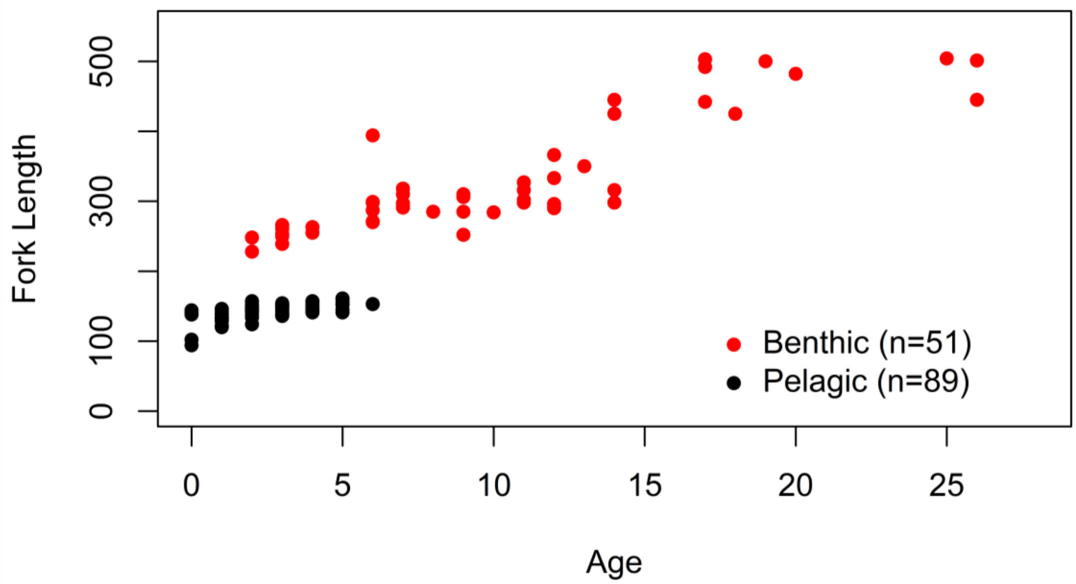

Figure 8. Age (years) and fork length (mm) of the two lake whitefish forms in Big Trout Lake, Algonquin Provincial Park, Ontario.

The Big Trout Lake pair of lake whitefish represents the eighth occurrence of this phenomenon in Canada (Mee et al. 2015). In recognition of these unique cases of *island evolution*, COSEWIC (Committee on the Status of Endangered Wildlife in Canada) recognizes the status of designatable unit as a means of assigning status to populations that are evolutionarily unique within a broader species distribution. A similar phenomenon occurs with threespine stickleback in several lakes on the west coast of Canada. In these cases, sticklebacks that occupy pelagic and benthic lake habitat are reproductively isolated, adopt different foraging niches, and occupy different food web positions. They are functionally different species stemming from ecological speciation (Schluter 1996) and are designatable units in COSEWIC evaluations.

In four lakes — Cedar, Radiant, Hogan, and Mink — unique forms of cisco occur, with one being the ancestral form and the other appearing to be the blackfin cisco form that historically occurred in the Laurentian Great Lakes (Bell et al. 2019; Figure 9). Because they occur in lakes once part of glacial Lake Algonquin drainage, the possible blackfin cisco form may be relics from nearly 13,000 years ago (Bell et al. 2019). The blackfin cisco that occupied the Laurentian Great Lakes is red-listed as extinct by the IUCN and is currently listed as data deficient by COSEWIC and COSSARO (Committee on Status Species at Risk in Ontario).

Closer examination of the blackfin form feeding structure in each lake and their genetic profile reveal the blackfin form of cisco in Algonquin Park to be unique, resulting from independent evolution in each lake (Bell et al. 2019, Piette-Lauzière et al. 2019). The ancestral form of cisco and the blackfin form in each lake are more closely related to each other than to other similar forms in other lakes. All cisco in Algonquin Park possess a genetic profile that does not match the Laurentian Great Lakes as recognized today so they are not colonizers from that lake system. Rather, their genetic profile points to cisco in the park as being founded during the era of Lake Algonquin. The presence of evolved forms of cisco in the park is a unique feature of the park's fish fauna.

Figure 9. A blackfin form of cisco from Radiant Lake, Algonquin Provincial Park, Ontario (Bell et al. 2019).

Conservation metrics for freshwater ecosystems

Conservation metrics can be based on several criteria for ranking or prioritizing features of aquatic ecosystems that are important for maintaining ecological integrity. For example, maintaining native species and food web representativeness are important elements of ecological integrity. The relative representation of native fish and their life histories is an approach to conservation planning (Strecker et al. 2011). Food web structure in park lakes could be represented by the spectrum of fish sizes that reveals a food web balance among predators and prey (Chu et al. 2017). Loss of predatory or prey fish would alter this balance and therefore alter lake productivity. Prioritizing requires an understanding of what is available on the landscape or in the aquatic network and assigning relative importance to different features. The fish species and food web variation in lakes of Algonquin Park serve as examples.

Since the unique forms of cisco or lake whitefish that meet criteria for designatable units under COSEWIC (see previous section) may be important for the ecological integrity of Algonquin Park, lakes with these populations would be ranked high relative to lakes with normal cisco and lake whitefish. In this case, ecological integrity would be based on the continued persistence of these populations.

Based on the structure of the prey field, all lake trout food web types may be ranked as high in maintaining ecological integrity. This example recognizes the importance of food web diversity and the corresponding effects on lake trout life history. Food web diversity is a metric that can be maintained by limiting the introduction of fish to the park landscape. Measures of lake isolation from access points or park boundaries where fish introductions are more likely may also be part of this ranking process. This would allow sets of lakes with varying likelihood of maintaining food web diversity for lake trout to be identified.

Similarly, self-sustaining brook trout populations in lakes are of conservation concern so park lakes with self-sustaining brook trout may be ranked high in terms of meeting ecological integrity goals. Lakes with self-sustaining brook trout but without introduced predators may be ranked even higher and lakes without competitors such as yellow perch ranked higher still (Browne and Rasmussen 2009).

Another approach is to recognize that introduced predatory fish disrupt native food webs and potentially eliminate native species. The number of introduced predatory species is a basic measure of the degree of food web change (see Figure 3). Rock and Booth lakes are two examples. Multiple predator introductions have occurred in Booth Lake (i.e., smallmouth bass and northern pike) and Rock Lake (largemouth bass, smallmouth bass, rock bass, and possibly walleye). These predators capture inshore fish production and are known to reduce or eliminate fish species from lakes in the park (MacRae and Jackson 2001, Jackson 2002). Movement downstream or upstream by introduced predators from these lakes risks the spread of introduced predators to other lakes. Ecological integrity is reduced in these and other lakes with introduced predators with respect to a reference state represented by most lakes in the interior of Algonquin Park.

Aquatic conservation planning principles

Management of parks and protected areas includes planning and implementation as a continuous cycle of engagement (indigenous communities, stakeholders, and the public), decision making, evaluation, and reporting. Conservation planning as a component of this planning and implementation cycle should include:

1) identifying and locating conservation priorities such as species at risk, species of broad interest or representation, and unique aquatic food webs
2) mapping the distribution of target species or habitats and assessing their representation in a larger landscape
3) determining ways to protect features subject to trade-offs based on cost, effectiveness, and representation

A suite of planning approaches exists for terrestrial ecosystems but much less so for aquatic ecosystems. Current terrestrial protected areas may also protect aquatic ecosystems to some extent (Chu et al. 2017) but not others (Azevedo-Santos et al. 2019). The broad sense is that terrestrial approaches to conservation planning do not adequately represent the network and directional flow of watersheds that many aquatic species rely on (Flitcroft et al. 2019 and companion articles).

Recent reviews of freshwater conservation planning highlight conceptual advances in this area, including a consensus on the need to address this topic (Flitcroft et al. 2019). Several initiatives and analyses of aquatic fauna and watersheds are providing the elements of what can be described as aquatic or freshwater conservation planning (Linke et al. 2008), including examples in California (Howard et al. 2018), southeastern United States (Thieme et al. 2016), and South America (Tognelli et al. 2019).

Aquatic conservation planning differs in several ways from conservation planning for terrestrial ecosystems. As described earlier, aquatic connectivity among lakes of Algonquin Park occurs within watersheds best described as directional nested networks (Melles et al. 2012, 2014). Aquatic connectivity is generally considered to be focused on streams and rivers. Algonquin Park presents a more complex challenge for aquatic conservation planning beyond approaches focusing on streams and rivers. The complex of lakes, wetlands, and tributary linkages that make up the directional nested network of aquatic ecosystems in the park influence aquatic connectivity through factors such as changes in temperature or productivity as well as movements of fish among these elements of the park's aquatic ecosystems (Jones 2010, Jones and Schmidt 2017). In terrestrial conservation planning, at some level is an assumption of independence of sites or locations identified for planning purposes. This stems from the basic differences between terrestrial and aquatic ecosystems (see Figure 2 and Table 3).

The dynamic nature of directional nested networks leads to several principles to consider in aquatic planning (Nel et al. 2011, Adams et al. 2015, Hermoso et al. 2016):

1) Select areas with **high ecological integrity,** meaning areas that encompass natural variation in abiotic and biotic processes observed in natural aquatic ecosystems. Natural variation is high in several features of aquatic ecosystems. Annual patterns of snow melt and water flow along with seasonal patterns of ecosystem productivity among lakes, wetlands, and streams (low in winter; high in summer) need to be recognized to maintain naturally functioning aquatic ecosystems.

2) Incorporate **connectivity** into planning related to native and introduced species. Time lags exist in how species introductions or environmental effects propagate through a watershed so spread from one aquatic site to another in a different location in a watershed needs to be understood. Any time lag or spread will be based on the site of introduction or environmental damage. With connectivity and barriers, introductions at a lower elevation point in a directional nested network may produce different outcomes with respect to spread than those occurring at a higher elevation in a network.

3) **Fully incorporate areas or habitats needed for population persistence** of aquatic organisms. In the case of brook trout, for example, this will include areas of groundwater recharge and discharge. Seasonally flooded habitat is important for many fish species.

4) Whenever possible, **map natural processes that can affect aquatic ecosystems** because they likely affect the persistence of many aquatic species. Lack of detailed information on species distributions for many aquatic species may necessitate mapping features such as wetlands, water depth, surficial geology, slope, and water flow as surrogates for predicting species distributions.

5) Account for the full effects of **introduced species**, which do not contribute to high ecological integrity because of their effects on native species abundance and natural processes such as predator/prey relationships that exist among long standing, post-glacial fish assemblages. Measures of ecological integrity that focus only on physical-chemical parameters or treat introduced species as like species in native fish assemblages fail to consider the full effects of species introductions (Hermoso et al. 2011, Hermoso and Clavero 2013).

In northwestern Ontario, a ranking of fish species based on five criteria has produced a species list very similar to the fish species found in Algonquin Park (McDermid et al. 2015). The rankings are based on: 1) whether a species is widely distributed; 2) whether species are cool- and coldwater species; 3) the species' importance to indigenous peoples and anglers; 4) the habitats used by different fish species and whether any are habitat specialists; and 5) the vulnerability of different fish species to, for example, forestry, hydroelectric development, mining, and climate change. Most species are considered cold water or cool water adapted, are widespread, and occupy lakes but use rivers seasonally (McDermid et al. 2015).

Table 5 summarizes the rankings of fish from northwestern Ontario and their similarity to those from Algonquin Park. All species are widely distributed in the northwest and subject to one or all of the criteria listed as important in rankings. In Algonquin Park, lake sturgeon (rank 1), walleye (rank 3), and northern pike (rank 6) have limited distributions. Northern pike have been introduced to the park, walleye is native to the lower Petawawa River (Lake Travers and downstream) and introduced elsewhere, while lake sturgeon has been noted in McManus and Whitson lakes based on the detection of one dead fish.

The remaining species are native to Algonquin Park and widely distributed within its boundaries (Ridgway et al. 2017). Lake trout, brook trout, lake whitefish, cisco, and burbot are coldwater fish and are projected to be affected by climate change and species introductions — two factors threatening the future of fish in the park. Species on this list of coldwater species have been detected in rivers in Algonquin Park, but only brook trout are found in all fourth order watersheds and fulfill some or all their life history stages in rivers, lakes, or both. Brook trout are therefore a primary element in aquatic conservation planning in Algonquin Park along with the other coldwater fish species.

Information about the distribution of other aquatic species such as amphibians and invertebrates are less available than that for fish, for which spatial coverage is poor in many regions. This can limit the utility of aquatic conservation planning. In the absence of detailed species level information, ranking areas based on species richness at regional or watershed scale, the number of species at risk known to be in an area, and landscape diversity — preferably at watershed scale — are several ways to address conservation planning in the absence of detailed information (Hermoso et al. 2016).

The use of indicator species may be an interim option to overcome lack of information about many aquatic species. While some advocate for this approach, close examination of the utility of using one group to infer priority areas for another points to several limitations. In one study, using fish, amphibians, and freshwater mussels to select priority conservation areas resulted in different areas for aquatic conservation for each group, with only 20% overlap

Table 5. The rank order of fish species as candidates for aquatic conservation planning in northwestern Ontario based on McDermid et al. (2015) and their relevance for Algonquin Park. Distribution of native lake sturgeon and walleye are limited and northern pike is an introduced species in the park. ●=yes; ○=no. Lake sturgeon (*) is listed as being in the park based on fish observed in McManus and Whitson lakes; walleye (*) is based on native occurrence in Lake Travers; northern pike (*) is based on an old observation in Basin Lake so it is not known if this species is native to the park.

Species	Rank	Historical presence	Native species	Currently present	Widely distributed
Lake sturgeon	1	●	●	●*	○
Lake trout	2	●	●	●	●
Walleye	3	●	●	●*	○
Brook trout	4	●	●	●	●
Lake whitefish	5	●	●	●	●
Northern pike	6	●*○	○*	●	○
Cisco	7	●	●	●	●
Yellow perch	8	●	●	●	●
White sucker	9	●	●	●	●
Burbot	10	●	●	●	●

(Stewart et al. 2018). Selecting conservation areas for one aquatic group is not likely to protect other groups. More generally, use of indicator species, or coarse surrogates such as habitat or environmental classification, implies that the relationship between the indicator and drivers of environmental change or biodiversity change are understood and closely linked (Lindenmayer and Likens 2010). Linking the indicator to change and drawing broad-based conclusions can be tenuous in the absence of a deeper understanding of the ecology of species of interest.

Despite these limitations, Algonquin Park is well situated for aquatic conservation planning given our current understanding of fish distribution, watershed boundaries and connectivity, and the role of the Algonquin Dome in producing headwaters for several major river systems in southern Ontario.

Algonquin Park and aquatic conservation planning

Few protected areas in North America can match Algonquin Park for its role in aquatic conservation (Lawrence et al. 2011). Current park boundaries encompass the Algonquin Dome, which is the source of several watersheds, affording them protection. Fish species distribution and their associated watershed boundaries are well understood (Ridgway et al. 2017). Aquatic connectivity is mapped with risk of fish introductions identified. This level of insight contrasts with many areas for which basic information about fish distribution, their habitats, and aquatic connectivity is lacking. Such knowledge impediments are widely recognized and can restrict aquatic conservation planning in many areas of the world (Stiassny 2002).

Algonquin Park is a candidate for aquatic conservation planning because:

1) Several watersheds begin in the protected area of the Algonquin Dome. This protection makes watershed-based planning more feasible and is consistent with the number one goal for Algonquin Park when it was established in 1893.
2) Watershed connectivity in the park is well understood, including barriers that afford protection from invasive species.
3) Access to the park landscape is limited, providing a relatively high level of protection from disturbance.
4) Distribution of the native and introduced fish fauna is well known, including the glacial history contributing to their present-day distribution.
5) Brook trout and lake trout populations are concentrated among many of the park’s lakes, making the park important for their conservation.
6) Unique forms of cisco and lake whitefish not found elsewhere in Ontario or Canada exist in seven park lakes.
7) Two important stressors, climate warming and introduced species, are affecting the park and their effects on ecological integrity can be assessed.
8) The park has relatively high aquatic ecological integrity over most of its watersheds and serves as a reference condition for comparison at several scales. Within its own boundaries and beyond, areas of introduced fish and associated risks to native species can be compared with those in the park to assess loss of ecological integrity in other areas in Ontario. Brook trout and lake trout population levels in the park can serve as a reference state for other areas of the province.
9) A wealth of information is available about the park from mapped databases and aquatic ecology research acquired over decades of field monitoring and research, making conservation planning feasible.

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