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A science and management partnership to restore coregonine diversity to the Laurentian Great Lakes

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Abstract

Similar to many freshwater ecosystems, the Laurentian Great Lakes of North America have undergone numerous anthropogenic stressors resulting in considerable loss of biodiversity and habitat. Among Great Lakes fishes, the coregonine subfamily has endured the most extensive declines, including extinction of several species (*Coregonus johannae*, *C. alpenae*, and *C. kiyi orientalis*) and at least 10 instances of local extirpations of other species (*C. nigripinnis*, *C. reighardi*, *C. zenithicus*, *C. hoyi*, and *C. artedi*) across all 5 lakes, much of which occurred prior to the 1960s owing to overfishing, interactions with non-indigenous species, and habitat loss. Despite these declines, no federal-, provincial-, or state-mandated actions were ever implemented to conserve coregonine diversity, potentially because so much of the coregonine declines occurred prior to the enactment of federal conservation legislation. Possible explanations for inaction since enactment of that legislation include insufficient data on biological vulnerability or threats, unresolved taxonomy, and limited support from the fishery management agencies and their stakeholders prior to the 2000s. In recent decades, however, several fishery management agencies have undertaken efforts to re-introduce coregonine diversity. These efforts helped lead to development of a science-based framework to restore coregonines that was universally endorsed by fishery managers representing eight U.S. states, four U.S. tribal organizations, and the province of ON, Canada, in May 2018. The basin-wide framework is based on principles of conservation biology and adaptive management. We describe details of its key steps, including planning, restoring, and evaluating, while also describing recent implementation efforts to develop methods, improve available resources, and enhance coordination across the basin. Although our paper describes a regional effort to restore native coregonines, our adaptive-management approach could be used by other multi-agency stakeholders seeking to conserve or restore native fishes.

Key words: native fish, conservation, adaptive management, fish management, stakeholder

Introduction

Freshwater ecosystems have endured a litany of stressors (e.g., physical alteration, eutrophication, biological invasion, and climate change) over the past century that have led to the loss of both habitat and biodiversity, including fishes (Revenga et al. 2005; Ormerod et al. 2010; Gordon et al. 2018; Reid et al. 2019) at multiple trophic levels. As water quality has generally improved in North America (e.g., Anderson et al. 2005; Katz et al. 2007; Schindler 2012) and laws have codified the conservation of species at risk of extinction and their habitats [e.g., Endangered Species Act (ESA) 1973 in the United States (US) and Species at Risk Act (SARA) 2002 in Canada], efforts to conserve remaining fish diversity and their habitats or even initiate restoration programs can occur through a variety of processes. At the federal level, Canadian efforts are driven by the assessment of conservation status by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC), which can assess species and designatable units (equivalent to evolutionarily significant units) as special concern, threatened,

Fig. 1. Map of the Laurentian Great Lakes basin with demarcation of state, provincial, and international borders in the United States (USA) and Canada (CA), as well as some of the locations referenced in this paper. Inset: Map of North America highlighting the Laurentian Great Lakes region (box). This map includes two publicly available layers: a Great Lakes shoreline layer downloaded from the Great Lakes Aquatic Habitat Framework (https://www.glahf.org/) and a North American Political Boundaries layer (https://www.sciencebase.gov/catalog/item/4fb555ebe4b04cb937751db9).

endangered, extirpated, extinct, not at risk, or data deficient. Under SARA, the government must develop recovery strategies or action plans for species assessed as threatened, endangered, or extirpated by COSEWIC; for species assessed as special concern by COSEWIC, management plans must be developed. Likewise, in the US, fishes that are listed as threatened or endangered under ESA trigger a series of planning and regulatory actions, including development of species recovery plans. Furthermore, non-federal jurisdictions may have their own codified efforts to conserve fish species and habitats important to their sustainability. Multijurisdictional commissions are another entity that can sustain and protect fishes, most commonly interjurisdictional migratory species (e.g., Pacific Salmon Commission, Connecticut River Atlantic Salmon Commission, and Susquehanna River Anadromous Fish Restoration Cooperative). Finally, voluntary partnerships can arise, such as the Candidate Conservation Agreements in the US (see Donlan 2015), which proactively seek to recover fish species to prevent future listing under ESA.

The Laurentian Great Lakes (hereafter, Great Lakes, see Fig. 1) are illustrative of many freshwater ecosystems that have endured a series of anthropogenic stressors since European colonization. Overfishing, habitat degradation, pollution, and the negative impact of non-indigenous species have been key drivers underlying a decline in fish biodiversity (Eshenroder and Burnham-Curtis 1999; Mandrak and Cudmore 2010; Allan et al. 2013). In the Canadian waters of the Great Lakes, 45 fish species and designatable units have been assessed and assigned a conservation status by COSEWIC, and most of these species are listed under SARA. Conversely, in the US, no Great Lakes fish species is currently listed under ESA, although the status of Lake Sturgeon (*Acipenser fulvescens*) is "Under Review" (Laura Ragan, USFWS, personal communication, 23 March 2023). As a result, codified efforts to conserve native fishes in the Great Lakes basin, to date, have been based primarily on the SARA process in Canada, and actions undertaken by individual state, provincial, or tribal entities. Conservation or restoration efforts for Great Lakes species not listed under SARA (or ESA) have involved cooperation within the Joint Strategic Plan (JSP) process (described in detail later), which involves the entities with management authority across the Great Lakes (eight US states, four US tribal organizations, and the province of ON) and support from the Great Lakes Fishery Commission (GLFC), US and Canadian federal agencies, and academic institutions.

Restoration of lake trout *Salvelinus namaycush*, a native top predator, was the first basin-wide, cooperative conservation or recovery effort undertaken within the JSP. Lake trout fishery yields collapsed in all lakes during the 1940s and 1950s due to overexploitation, parasitism by invasive sea lamprey *Petromyzon marinus*, and habitat degradation. The only stocks that persisted were in offshore Lake Superior and a few isolated regions of Lake Huron (Hansen 1999; Muir et al. 2012). Management recovery efforts focused on sea lamprey control, stocking of lake trout, and fisheries regulations (including the creation of refuges) while also benefitting from a decline in the abundance of invasive alewife *Alosa pseudoharengus* that can limit lake trout recruitment success (Holey et al. 1995; Krueger et al. 1995; Hansen 1999; Riley et al. 2011). Over the past 30 years, lake trout have re-established self-sustaining populations in Lake Superior (Hansen et al. 1995; Hansen and Bronte 2019), and naturally reproduced fishes now comprise 50% of younger cohorts in Lake Huron (Johnson et al. 2015*a*). Recovery efforts continue in the other lakes with lesser degrees of success. With hindsight, scientists and managers can recount several lessons over more than 50 years of recovery effort and have identified the need for interagency coordination, stakeholder engagement, clear milestones to restoration goals, comprehensive monitoring, and an adaptive framework that facilitates opportunities to revisit strategies and goals (Bronte et al. 2017).

The Coregoninae sub-family of ciscoes and whitefishes and their habitats in the Great Lakes were also severely impacted by anthropogenic stressors. In a recent synthesis of ciscoes in the Great Lakes, for example, Eshenroder et al. (2016) reported that at least 70% of their diversity has been lost. Overfishing is typically cited as the first driver underlying the declines (Christie 1972; Smith 1972; Eshenroder et al. 2016). For example, in Lake Michigan, the first species to become extirpated were the largest and most heavily targeted by fisheries (Smith 1964). Negative interactions with invasive species have also been hypothesized to have contributed to the loss of species. For example, parasitic sea lamprey typically target the largest fishes for blood meal and likely contributed to the decline of lake whitefish (*C. clupeaformis*) and even some of the larger cisco species (Christie 1973; Eshenroder and Burnham-Curtis 1999). Non-indigenous planktivorous fishes (e.g., alewife and rainbow smelt *Osmerus mordax*) also began increasing in abundance from the 1880s through 1960s (depending on the lake), although the importance of their effects on the decline of coregonines has been debated (e.g., Christie 1974; Crowder 1980; Madenjian et al. 2008; Myers et al. 2009). Finally, habitat degradation has almost certainly contributed to declines in coregonine diversity, although the mechanisms have not been as well defined and studied as in European systems. For example, in the Great Lakes we surmise that the loss of many river-spawning stocks (see citations in Schaefer et al. 2022) was due to the construction of dams in most tributaries. Likewise, deforestation and conversion of land to agriculture led to high sedimentation inputs in the 19th and early 20th century (e.g., Lawrie and Rahrer 1973; Bogue 2000; Fitzpatrick and Knox 2000). Although many fisheries still had high landings up through the 1950s, it remains unclear how this habitat degradation limited fish production, and ongoing work is seeking to evaluate whether excessive sedimentation is now limiting spawning habitat quality in Lake Ontario, as has been documented in Europe (Ventling-Schwank and Livingstone 1994). Excessive nutrient inputs during the mid-20th century also were hypothesized to limit coregonine egg survival, especially in embayments (see Madenjian et al. 2011). As the abundance and distribution of these species declined, hybridization and introgression may have occurred among the remaining species (Smith 1964; Todd and Stedman 1989; Eshenroder et al. 2016), potentially reducing the remaining biodiversity.

Despite the losses of coregonine diversity, recovery efforts have lagged decades behind those for Lake Trout, and federal conservation classifications have differed between the US and Canada (Table 1). For example, Canada has listed two species/designatable units as extinct [Deepwater Cisco (*Coregonus johannae*) and Kiyi in Lake Ontario (*C. kiyi orientalis*)]. Likewise, Shortnose Cisco (*C. reighardi*) was assessed as endangered, but recovery was not considered feasible given that it has not been documented in the wild since 1985 (Fisheries and Oceans Canada 2012). Shortjaw Cisco (*C. zenithicus*) was assessed as threatened (COSEWIC 2003) but has not been listed under SARA owing to lack of data and unresolved taxonomy. Finally, Kiyi in lakes Superior and Huron (*C. kiyi kiyi*) is listed as special concern in Canada and has a management plan (Fisheries and Oceans Canada 2016), but, to our knowledge, no specific actions have been implemented to date. In the US, persuasive evidence for extinction was acknowledged (Federal Register 1989) for Deepwater Cisco, Blackfin Cisco (*C. nigripinnis*), and Longjaw Cisco (*C. alpenae*). Information also indicated that proposing to list *C. kiyi* (no distinction was made among Kiyi among the Great Lakes), Shortnose Cisco, and Shortjaw Cisco was "possibly appropriate" but that "conclusive data on biological vulnerability and threat are not currently available to support proposed rules" (i.e., Category 2 candidate species; Federal Register 1989, 1994). In 1996, the US Fish and Wildlife Service (USFWS) discontinued the list of Category 2 candidate species (i.e., species for which conclusive data on vulnerability and threat not currently available to support rules) and instead focused efforts on working with the States and other private and public interests to assess their need for protection under the ESA (Federal Register 1996). Since that time, several status assessments for Shortjaw Cisco have been drafted, but no further actions have been taken (Laura Ragan, USFWS, personal communication, 24 October 2022). As a result, any new efforts to conserve coregonine diversity and their habitats would occur outside of any active federal regulatory authority.

Despite the lack of agency-mandated actions, Great Lakes fishery managers have increasingly expressed support for cooperative actions to foster resilient coregonine assemblages to support diverse fisheries, reestablish lost trophic linkages, and identify and restore key habitat. These activities culminated in fishery managers at the basin-wide level endorsing a science-based framework to restore coregonines in the Great Lakes [Fig. 2, herein, Coregonine Restoration Framework (CRF)] on 1 May 2018 (Brian Locke, Ontario Ministry of Natural Resources and Forestry, Chair of the Council of Lake Committees, personal communication, 13 April 2023). We emphasize that even though the framework specifies restoration (i.e., re-establishing locally extir-

Table 1. Summary of Canadian and United States (US) status of cisco species in the Laurentian Great Lakes, including in which lakes each species originally occurred based on Eshenroder et al. (2016).

Species name	Common name	Lakes where once occurred	Canadian status	US status or activity
C. alpenae	Longjaw Cisco	Michigan, Huron, Erie	Not assessed[a]	Evidence for extinction
C. artedi	Cisco	Superior, Michigan, Huron, Erie, Ontario	Not assessed	Not assessed
C. hoyi	Bloater	Superior, Michigan, Huron, Ontario	Not at risk	Not assessed
C. johannae	Deepwater Cisco	Michigan, Huron	Extinct	Evidence for extinction
C. kiyi	Kiyi		See subspecies below	Former Category 2 candidate species[b]
C. kiyi kiyi	Kiyi	Superior, Michigan, Huron	Special concern[c]	
C. kiyi orientalis	Kiyi	Ontario	Extinct[d]	
C. nigripinnis	Blackfin Cisco	Superior[e], Michigan, Huron	Data deficient	Evidence for extinction
C. reighardi	Shortnose Cisco	Superior[e], Michigan, Huron, Ontario	Endangered	Former Category 2 candidate species[b]
C. zenithicus	Shortjaw Cisco	Superior, Michigan, Huron	Threatened[f]	Former Category 2 candidate species[b]; status assessments drafted as recently as 2012 but no further action taken

Note: In Canada, status is assessed by Committee on the Status of Endangered Wildlife in Canada (COSEWIC) under the Species at Risk Act (SARA), and in the US assessment occurs under the Endangered Species Act (ESA).
[a]Was proposed to be synonymous with *C. zenithicus* by Bailey and Smith (1981) and, therefore, not considered a valid species for assessment by Canada (see: https://species-registry.canada.ca/index-en.html#/species/70-542).
[b]Defined as "conclusive data on biological vulnerability and threat not currently available to support rules".
[c]*C. kiyi kiyi* subspecies assessed only by COSEWIC (2005).
[d]*C. kiyi orientalis* subspecies assessed only by COSEWIC (2005).
[e]Described as "Uncertain" as to whether it occurred or occurs in Superior by Eshenroder et al. (2016).
[f]Assessed as Threatened by COSEWIC (2003) but not listed under SARA.

pated species), the framework can also be applied to conserve existing stocks of management concern. This perspectives paper seeks to provide a broad overview of the CRF, spanning from its development to its implementation, and is divided into five sections. The first provides a brief background on how cooperative fisheries management is achieved in the Great Lakes. The second is organized by each of the five Great Lakes and describes what diversity and habitat have been lost and any relevant contemporary fishery management perspectives. The third section provides more details regarding how fishery managers became motivated to restore coregonine diversity and key milestones on the pathway to basin-wide endorsement of the CRF. The fourth section unpacks the details of the CRF, including its foundational principles and descriptions of the three key steps that follow its adaptive management approach. Finally, the last section describes current efforts to implement the CRF strategy. By describing the motivation, development and endorsement of this framework to restore or conserve native species and their habitats, we also seek to inspire other multi-agency stakeholders that are exploring a similar objective outside of a government-mandated process.

Cooperative fishery management in the Great Lakes

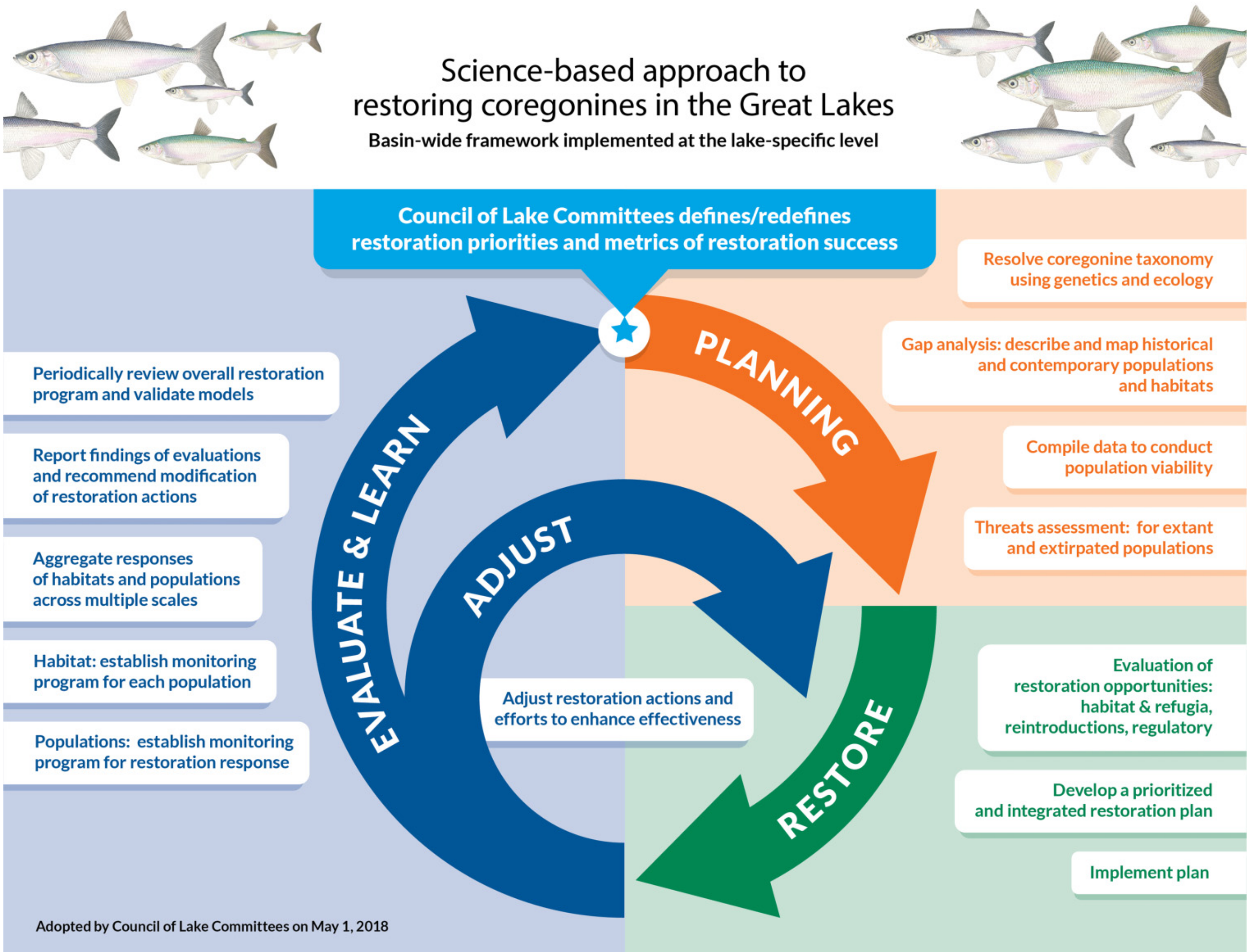
The history of cooperative fishery management in the Great Lakes is filled with fits and starts (Gaden 2016). Jurisdictions recognized that fishes moved across jurisdictional boundaries but did not want to relinquish their sovereign authority. Beginning in the mid-1800s and continuing through the mid-1900s, overfishing, habitat degradation, and invasive species collectively reduced production of valued fishes throughout the Great Lakes (Smith 1968, 1972). The GLFC was established in 1955 after Canada and the United States signed the *Convention on Great Lakes Fisheries* in 1954 (U.S. Department of State 1956). By 1963, the GLFC established lake committees as fora for fishery managers to share information, coordinate their management programs, and advise the GLFC about the execution of its research programs.

These early lake committees established a culture of cooperation that set the stage for strategic cooperation through *A Joint Strategic Plan for Management of Great Lakes Fisheries* (hereafter, JSP), which went into effect in 1981 (GLFC 2007). The JSP, signed by state, provincial, tribal, and federal fishery management agencies, commits agencies to strategic cooperation without abrogating any individual jurisdictional authorities or responsibilities. Within the JSP, agencies operate by consensus, share information, provide regular reports, and seek to influence ecosystem management to sustain fish production. The GLFC facilitates the process. Under the JSP, signatory agencies agree to work together within individual lakes as lake committees, each of which has established Fish Community Objectives (FCOs) that express the desired state of fish populations of common concern in each lake. In addition, a Council of Lake Committees (CLC) was established in 1978 to consider issues affecting two or more lakes. The JSP was well exercised in the interjurisdictional effort to restore lake trout (i.e., Muir et al. 2012; Hansen and Bronte 2019).

Cisco diversity in the Great Lakes

Because the original intent of the CRF was to be inclusive of all Great Lakes coregonine species, which includes several cisco species and three "whitefish" species (*C. clupeaformis*,

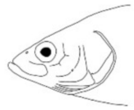
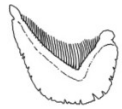
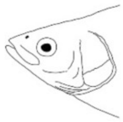
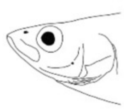
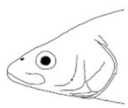
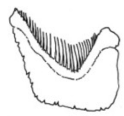
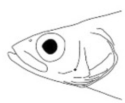
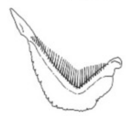
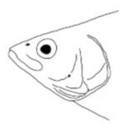
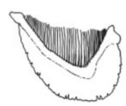
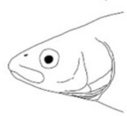
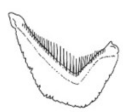
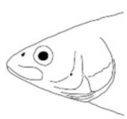
Fig. 2. Coregonine Restoration Framework endorsed basin-wide by Great Lakes fishery managers on 1 May 2018 (Brian Locke, Ontario Ministry of Natural Resources and Forestry, Chair of the Council of Lake Committees, personal communication, 13 April 2023), whereby the managers define (or redefine) restoration priorities and metrics of success that is operationalized by planning (orange; upper right), restoring (green; lower right), evaluating, learning, and adjusting (blue; left half).



Prosopium cylindraceum, and *P. coulterii*), we continue to maintain "Coregonine" as the first name of the framework. The current focus and application of the CRF, however, is to restore or conserve the diversity of ciscoes (note lack of capitalization). Hence, for expediency and brevity, any subsequent references to "coregonine" in this paper will refer only to ciscoes, which can occupy both relatively shallow (including riverine) and deep-water habitats, attain different sizes, spawn at different times of the year, and be morphologically distinguished based largely on differences in head and body shape, paired fin lengths, and gill raker characteristics (see Table 2).

The biodiversity of ciscoes has been substantially reduced since Koelz (1929) first described the coregonine fishes of the Great Lakes. Taxonomically, seven species of ciscoes that are currently recognized in Page et al. (2013) are now, or were once, found in the Great Lakes. Since Koelz (1929), Todd and Smith (1992) and Eshenroder et al. (2016) have updated the status of ciscoes across the Great Lakes. In the last update, Longjaw Cisco was re-recognized after being synonymized with Shortjaw Cisco by Bailey and Smith (1981); hence, in Table 2 of Eshenroder et al. (2016), they described 28 occurrences of 8 cisco species occurring across all 5 of the Great Lakes. They concluded only 8 occurrences remain extant—a 71% reduction in diversity. Eshenroder et al. (2016) also hypothesized that some of the species in Lake Huron have hybridized and undergone introgression. Although the CRF includes a process intended to resolve the taxonomic uncertainty, in this manuscript we refer to species names out of convenience rather than to reflect taxonomy, following Eshenroder et al. (2016), and capitalize the common names to avoid confusion with the generic term "cisco or ciscoes". Below, we seek to enhance lake-specific summaries compiled by Eshenroder et al. (2016) by (1) summarizing subsequent research that has advanced understanding in morphological, functional, or genetic diversity of ciscoes and (2) describing current fishery management perspectives on coregonine restoration or conservation. Although these sections are organized by lake, we also highlight the connections between lakes (see Fig. 1) that in many cases also rep-

Table 2. A summary of key taxonomic and ecological traits for eight ciscoes (*Coregonus* spp.) originally described in the Great Lakes, with the common cisco name following the species name.

Taxa	Head profile	Gill raker profile	Mean # gill rakers (range)	Spawning time	Bottom depth (m) (April-Nov)	Mean total length (mm) [95th percentile]
C. alpenae Longjaw			38 (31-46)	November	69	304 [354]
C. artedi Cisco			47 (38-55)	November-December	30	297 [342]
C. hoyi Bloater			42 (37-50)	March	59	242 [304]
C. johannae Deepwater			29 (25-36)	August-September	97	296 [328]
C. kiyi Kiyi			40 (34-54)	October-November	142	267 [293]
C. nigripinnis Blackfin			46 (36-54)	December-January*	139	335 [412]
C. reighardi Shortnose			36 (30-43)	April-June	56	274 [301]
C. zenithicus Shortjaw			40 (32-46)	October-December	72	295 [340]

Note: Profiles of the head and gill rakers are reproduced with permission from Eshenroder et al. (2016). The mean number of gill rakers is from Appendix Table 1A of Eshenroder et al. (2016). The last three rows are each based on historical accounts from Lake Michigan, where all eight species once occurred. Spawning time is based on descriptions in Koelz (1929). Bottom depth, mean total length, and 95th percentile are based on model predictions (bottom depth) or summary statistics (length) of fishery-independent data collected during 1930–1932 (Bunnell et al. 2012; Kao et al. 2020). The asterisk for *C. nigripinnis* spawning time reflects uncertainty given that December–January is based on the account of two fishers and Koelz indicated that spawning was sometime between "October and March".

resent historical or contemporary habitat for Great Lakes coregonines and, based on European coregonine literature, could also serve as a vector for recolonization via larval drift (e.g., Naesje et al. 1986) or as migration corridor to a new habitat (e.g., Amundsen et al. 1999). Within the Great Lakes, the St. Marys River connects Lake Superior to Lake Huron, and there is no hydrological separation between Lake Michigan and Lake Huron. Lake Huron is connected to Lake Erie through the St. Clair River, Lake St. Clair, and the Detroit River. Finally, the Niagara River connects Lake Erie to Lake Ontario, but Niagara Falls restricts fish movement between these two lakes. Finally, Lake Ontario empties into the St. Lawrence River that ultimately reaches the Atlantic Ocean.

Lake Superior

Lake Superior has retained most of its historical assemblage of ciscoes, which currently comprises at least Cisco, Kiyi, Bloater, and Shortjaw Cisco (Table 1); the status of Blackfin Cisco and Shortnose Cisco is uncertain (Eshenroder et al. 2016), and current research is underway to assess whether these species occur in the lake. Lake Superior contains the largest standing stocks of Cisco in the Great Lakes, although biomass and rates of annual recruitment are likely currently below historical levels (Gorman 2012; Rook et al. 2021*a*). Commercial fisheries following post-European settlement principally targeted Cisco during spawning aggregations in November and December; fishing was also conducted during spring and summer, but these extractions were minor in comparison. Based on commercial fishery landings, stock sizes of Kiyi, Bloater, and Shortjaw Cisco in Lake Superior were smaller than those in Lake Michigan and Lake Huron (Baldwin et al. 2009; Bronte et al. 2010). In Lake Superior, Shortjaw Cisco was once the most abundant of the deepwater ciscoes in the historical fishery but now is the least encountered in fisheries and assessment surveys (Koelz 1929; Peck 1977; Bronte et al. 2010; Vinson et al. 2020). Although Lake Superior represents the headwaters of the Great Lakes basin and has undergone fewer anthropogenic disturbances than the downstream lakes, stock sizes of all ciscoes are likely below historical levels.

A renewed basin-wide interest in coregonine restoration has resulted in a renaissance of new discoveries in genetics and ecology and a rediscovery of previously reported research. Genomics has successfully delineated Lake Superior deepwater cisco species for the first time (Ackiss et al. 2020). Genetic differentiation coupled with recent evidence of trophic niche differentiation (Schmidt et al. 2011; Blanke et al. 2018; Rosinski et al. 2020; Bernal et al. 2022) and differential adaptation in vision genes that could explain differential habitat use (Eaton et al. 2021) suggest that formal species designations are justified. With respect to contemporary niche differentiation, minimal overlap was observed between non-native rainbow smelt and deepwater ciscoes (i.e, Kiyi, Bloater, and Cisco; Rosinski et al. 2020), which suggests that contemporary occurrence of rainbow smelt in other Great Lakes is not an insurmountable impediment to coregonine restoration efforts. Likewise, collections of Lake Superior larvae have also been identified to species using genomic methods (LaChance et al. 2021), not only opening new lines for early life-history research for Cisco, Kiyi, and Bloater but also demonstrating some differences in spatial and temporal emergence that could help explain how reproductive isolation has been maintained. Finally, a recent examination of Cisco spawning habitat use across the Great Lakes revealed a wide variety of habitat types used within Lake Superior, similar to what has been reported in the historical, primary, and anecdotal literature (Paufve et al. 2021). Cisco also likely historically spawned in Lake Superior tributaries (e.g., Gunderman and Baker 2008). Although future work to describe existing diversity (including possibly extant Blackfin and Shortnose Cisco populations) could be prioritized, Lake Superior and its (1) comparatively intact and diverse cisco complex and (2) less perturbed habitat can serve as a model or benchmark for comparative studies in the other lakes where existing ciscoes are reduced in diversity or distribution or when reintroductions are under consideration or being implemented. When appropriate, Lake Superior can serve as a gamete source for reintroductions into other Great Lakes where introgression is not a potential threat.

Lake Michigan

Once supporting an abundant and diverse community of eight cisco species (Table 1), Lake Michigan currently has just Bloater and Cisco remaining (Eshenroder et al. 2016). Bloater continue to inhabit the profundal and pelagic waters of the main basin, though recent estimates of abundance show substantial declines from population highs in the 1980s and 1990s (Collingsworth et al. 2014), and the commercial fishery is extremely limited compared to earlier decades. Today, Cisco abundance is much lower and its distribution more restricted relative to descriptions from early 1930s fishery-dependent and fishery-independent data, when Cisco was most concentrated in embayments such as Green Bay but also migrated to deeper waters during summer (Smith 1956; Kao et al. 2020). Cisco were extirpated from Green Bay by the 1960s; in 1984, Wisconsin Department of Natural Resources and University of Wisconsin–Milwaukee collaborated to stock ∼8000 Cisco into Green Bay, but there was no evidence of it being successful (F. Binkowski, University of Wisconsin-Milwaukee, personal communication, 23 March 2023). In contrast, contemporary data from multiple sources suggest that Cisco persisted in Grand Traverse Bay and has been expanding to other north and eastern Lake Michigan waters since 2011 (Claramunt et al. 2019), although recolonization into Green Bay has not yet occurred. Morphological comparisons using linear measurements between contemporary Grand Traverse Bay Cisco and Cisco measured by Koelz (1929) revealed notable differences with respect to head length, snout length, maxillary length, gill raker counts, and both dorsal and paired fin lengths, suggesting divergence from the historical form (Eshenroder et al. 2016).

Several recent ecological studies have also provided new insights regarding these contemporary Cisco, with some key differences compared to populations in other Great Lakes. For example, they are more piscivorous (Breaker et al. 2020) than individuals from most diet studies of Lake Superior Cisco (e.g., Gamble et al. 2011), although diets of Cisco >400 mm total length under the ice in Lake Superior revealed widespread piscivory (Hoff et al. 1997). Moreover, contemporary Lake Michigan Cisco have attained a larger body size and greater fecundity (Yule et al. 2020) than was historically estimated in Green Bay (1948–1952) or Lake Superior (1950–1954). In a cross-lake study of Cisco spawning, Paufve et al. (2021) reported egg deposition in relatively deep (15–30 m) waters with fine-grained substrate in Grand Traverse Bay, which was similar to observations in Thunder Bay, Lake Superior, and even shallower than recent observations near the Apostle Islands, Lake Superior (B. Weidel, personal communication, 9 September 2022) but differed substantially from the preference documented in Chaumont Bay, Lake Ontario, where Cisco spawned almost exclusively on relatively shallow (≤5 m), bedrock shoals. Future research should continue to describe existing diversity in Cisco spawning habitat, especially if increasing or reestablishing diversity in spawning habitat is identified as a restoration goal. Finally, Rook et al. (2021*b*) analyzed historical (1929–1970) commercial gill-net data from the Michigan waters of Lake Superior, Lake Huron, and Lake Michigan and reported no strong negative correlations between Cisco and lake whitefish, indicating that a fully restored cisco population would not likely be affected by lake whitefish (or vice versa).

Restoring native fish, such as coregonines, to increase the biological integrity of the fish community in Lake Michigan is an overarching goal in the FCOs (Eshenroder et al.

1995). Other potential benefits of a restored coregonine assemblage include diversification of the pelagic prey fish community, improved energy transfer across trophic levels and between nearshore and offshore habitats (sensu Ives et al. 2019), and the establishment of new commercial and recreational fisheries. A Native Planktivore Task Group established by the Lake Michigan Committee of the GLFC in 2013 was charged with critically exploring the feasibility of restoring Cisco and the once diverse assemblage of deep-water coregonines, but no substantive actions have been taken to date (V. Santucci, personal communication, 23 March 2023). Better understanding of extant Cisco populations has been cited as an important need for restoration planning in Lake Michigan (Broadway et al. 2019; Claramunt et al. 2019). Continued focus on critical unanswered questions, such as the threat of hybridization and introgression among coregonines, resolution of taxonomy to help inform decisions about potential source populations for reintroduction, and updated population viability assessments, could help Lake Michigan managers and stakeholders move coregonine restoration beyond the present early planning stages and into a potential implementation.

Lake Huron

Lake Huron, similar to Lake Michigan, once had the full complement of cisco species (Table 1) while also maintaining intraspecific diversity of Cisco—with a *manitoulinus* form exhibiting unique morphological characteristics within an embayment in North Channel (Koelz 1929; Eshenroder et al. 2021). Today, only two cisco species occur in Lake Huron: Cisco and Bloater. Bloater still occur lake-wide and exhibit high variation in abundance and recruitment (Collingsworth et al. 2014). Contemporary Bloater, however, have four morphological differences from those described by Koelz (1929), and Eshenroder et al. (2016) hypothesized that contemporary Bloater may instead be a hybrid resulting from introgression that occurred sometime after 1956. Historically, Cisco was one of the most abundant pelagic fishes, found "out of virtually every port on Lake Huron, in the North Channel, and Georgian Bay" (Koelz 1929). The current distribution of Cisco is limited to the St. Marys River, North Channel, Georgian Bay, and isolated regions within the main basin (e.g., Les Cheneaux Islands and the western side of the Bruce Peninsula; Cottrill et al. 2020; Eshenroder et al. 2021). Since major declines in abundance of Cisco populations in the 1950s, Cisco is no longer found in Saginaw Bay where it once supported the largest fishery in the lake (Baldwin et al. 2009). Contemporary Cisco continue to exhibit morphological variation (see Eshenroder et al. 2021), but whether this variation influences fishery management considerations may depend on whether morphological differences correspond to unique genetic stocks or to functional differences within the current altered ecosystem.

Of the two cisco species, fishery managers are currently more actively focused on Cisco than Bloater. The Lake Huron Committee has one FCO that aims to restore Cisco to a significant level and protect them where possible (DesJardine et al. 1995). Successful reintroduction of Cisco in Saginaw Bay may be critical to the overall recovery of Cisco in the main basin and provide multiple benefits: (1) diversifying the fish community and promoting sustainability of the food web, (2) establishing a larger-bodied prey fish that will reconnect the broken linkage between the nearshore and offshore energy pathways, (3) providing a prey buffer for other fishes such as yellow perch (*Perca flavescens*), and (4) potentially supporting its own future fisheries (Lake Huron Technical Committee 2023). As a result, the Lake Huron Committee initiated a multi-agency, Saginaw Bay reintroduction effort in 2018 that has resulted in the annual stocking of one million Cisco reared by USFWS, using northern Lake Huron populations as the gamete source (Lake Huron Technical Committee 2023). Cisco stocked in May or June (~5 months old) or October (~7.5 months old) receive differential marks to distinguish their survival rate. Both existing and new surveys are being used to capture stocked fishes (Lake Huron Technical Committee 2023). Adults were hypothesized to begin returning to Saginaw Bay in 2022 or 2023, and in December 2022, 46 marked adults (44 of them from the May or June release and 2 from the October release) were recaptured in Saginaw Bay (J. Bonilla-Gomez, USFWS, personal communication, 23 February 2023). Fishery managers strongly support new research and monitoring that can measure post-stocking mortality, characterize potential dispersal from stocking sites, estimate relative survival to maturity, and locate active spawning sites (R. Claramunt, personal communication, 23 March 2023). These evaluations are important for maximizing the success of Cisco reintroduction and for future management in Lake Huron.

Lake Erie

Historical descriptions of Lake Erie ciscoes included two forms of Cisco (a typical form and a deeper bodied "albus" form) and Longjaw Cisco (Koelz 1929; Scott and Smith 1962). The presence of only a single deepwater species is likely related to Erie being the shallowest Great Lake (maximum depth = 64 m), and its deepwater habitat being restricted to less than a third of its surface area (concentrated in the eastern basin). Among the two Cisco sub-species, the albus form was far more prevalent than the "typical" form, but albus has not been confirmed since 1957 and Cisco, regardless of form, is now rarely caught (Eshenroder et al. 2016). Between 1985 and 2015, fewer than 50 putative Ciscoes have been collected in fishery-independent and fishery-dependent sampling (CWTG 2016). Morphological and genetic analyses revealed some of these to be Bloater and Cisco from Lake Huron, and others were putative hybrids (CWTG 2016; Eshenroder et al. 2016; NEM and ASA, unpublished data). These findings, along with larval Cisco caught in the Detroit and St. Clair rivers in 2010–2013, suggest that the Ciscoes recently found in Lake Erie are likely the result of dispersal from Lake Huron, rather than being a small, isolated Erie population (CWTG 2016).

The albus was the largest Cisco form in the Great Lakes and, hence, the target of early fisheries and, consequently, the subject of early decline. At one point, the Cisco fishery in Lake Erie was considered one of the largest freshwater fisheries in the world, being fully developed by 1870 and averaging 12 000 tonnes per year from 1914 to 1924 (Koelz 1926). By 1927, landings declined to only 22% of the 1914–1924 average, and they were economically insignificant by 1928 (Van Oosten 1930; Eshenroder et al. 2016). Van Oosten (1930) blamed this "sudden collapse" of the fishery on unusual weather phenomena causing a large proportion of the lake's Cisco populations to concentrate in a deep hole off of Long Point in 1925 and intensive overfishing of that concentration, including removing a large number of sexually mature individuals before the spawning period. Landings remained low until 1946 when the catch briefly increased to 61% of the 1914–1924 harvest due to a very strong 1943-year class. In subsequent years, however, landings quickly declined to negligible values, with the last reported in 1965 (Baldwin et al. 2009).

The need for a Cisco rehabilitation plan for Lake Erie has been discussed since the early 2000s when a workshop was held to review the status of Cisco, and impediments to its recovery, in the Great Lakes (Fitzsimons and O'Gorman 2006). In the same year, two FCOs identified by the Lake Erie Committee (LEC) were relevant to Ciscoes, including (1) preventing the extinction of rare species and (2) maintaining a diversity of forage fishes to support predators and to sustain human use (Ryan et al. 2003). A rehabilitation plan to provide a framework for Cisco restoration was subsequently identified as a priority between 2004–2008 (Wills and Harris 2021). Early attempts to develop this plan were impeded by several information gaps, including the feasibility of stocking as a management option, identifying the most suitable broodstock, and genetic concerns related to stocking on a possible remnant population (CWTG 2015). As a precursor to the finalization of a Cisco rehabilitation plan for Lake Erie, the Lake Erie Coldwater Task Group was charged by the LEC with outlining possible impediments to Cisco rehabilitation, given the current and anticipated future status of Lake Erie (CWTG 2017). Rehabilitation impediments and knowledge gaps identified included climate change, invasive species, changes to the fish community and food web, and loss of critical habitats (CWTG 2017). The FCOs acknowledge that species of interest, such as Cisco, may present rehabilitation opportunities, but environmental conditions and fish community status will ultimately dictate the feasibility of restoration (Francis et al. 2020).

Lake Ontario

Lake Ontario once supported four cisco species (Table 1). By the middle of the 20th century, Shortnose Cisco, Bloater, and Kiyi were extirpated (Christie 1972), and the current distribution and abundance of Cisco are greatly reduced relative to historical levels. Most of the pelagic planktivore community is now dominated by non-indigenous fishes (e.g., alewife and rainbow smelt), although conserving Cisco and restoring deepwater ciscoes are objectives for Lake Ontario fish management (Stewart et al. 2017). Since the 1950s, Cisco recruitment has been sporadic, but abundance has generally declined (Weidel et al. 2021*a*). The extant Cisco population is primarily captured in northeastern regions, which coincides with spatial patterns in larval abundance and may suggest the habitat or conditions in the rest of the lake are no longer able to support all parts of the life cycle (Weidel et al. 2021*a*; Brown et al. 2022). Time series, cross-lake, and spatial patterns all support the hypothesis that the low and variable recruitment is heavily influenced by physical conditions such as variability in ice cover or spawning habitat degradation (Weidel et al. 2021*a*; Brown et al. 2022; Schaefer et al. 2022), although a less diverse complex of Cisco populations also could be a contributing factor (sensu Schindler et al. 2010). Morphologically, Eshenroder et al. (2016) reported minimal difference in eight metrics between a small sample of contemporary Cisco and what Koelz (1929) measured in Lake Ontario. Likewise, to date, there is no genetic evidence for differentiation among Cisco within Lake Ontario (George 2019).

Ecologically, Cisco in Lake Ontario are primarily zooplanktivorous, with non-indigenous invertebrates, *Bythotrephes* and *Cercopagis*, comprising much of their diet (Gatch et al. 2021). Cisco have not been observed in piscivore diets (Weidel et al. 2021*b*; Nawrocki et al. 2022). Spawning behavior in embayments is relatively well described and occurs on shallow (2–5 m) rock habitats (Pritchard 1931; George et al. 2017; Paufve et al. 2021), which differs from other Great Lakes populations (e.g., Dryer and Beil 1964; Smith 1956; Paufve et al. 2021). Experimental stockings as early as 2012 were attempted for only a few years to reestablish spawning populations in historical habitats (Connerton 2020), but priorities have shifted toward spawning habitat restoration to rehabilitate populations of Cisco and other native species (e.g., Lake Ontario Technical Committee 2022).

Among the ciscoes that were extirpated, Bloater has been the focus of recent and ongoing restoration efforts (Weidel et al. 2022). Historical information reveals that Bloater abundance sharply declined in the mid-1900s (Stone 1947) and surveys since 1978 had only captured one fish (in 1983, Weidel et al. 2022). To reintroduce Bloater into Lake Ontario, several agencies [Ontario Ministry of Natural Resources and Forestry, USFWS, U.S. Geological Survey (USGS)] have collaborated since 2012 to rear Bloater originating from Lake Michigan (see Holey et al. 2021) and have stocked more than one million fish to date (∼125 000 annually; Weidel et al. 2022). Telemetry studies found substantial predation on stocked fish (Klinard et al. 2020), suggesting restoration may be slowed by low post-release survival. Bloater recaptured in bottom-trawl surveys revealed that stocked fish use similar habitats and food resources as historical populations, but the low number of recaptures ($n = 10$) also indicates low survival of stocked fish (Weidel et al. 2022) or that too few fish are being stocked to generate returns. Weidel et al. (2022) noted that Bloater restoration in Lake Ontario could benefit from identifying the environmental conditions that contribute to successful Bloater reproduction in the upper Great Lakes as well as seeking to improve post-stocking survival through predator and food acclimation in the hatchery or acclimating stocked fish in the lake prior to release.

Pathway to a restoration framework

Given that coregonine diversity declined across the Great Lakes basin and their habitats have been substantially modified, initial discussions of shared motivations (e.g., restore historical diversity, conserve existing diversity, and address threats) occurred at the CLC level within the JSP process. As prey fish communities shifted over time, and in many cases underwent declines in total biomass, managers came to recognize that existing FCOs that sought diverse prey fish communities were trending in less desirable directions. As previously described in the lake accounts for Huron and Ontario, fishery managers began efforts to re-introduce ciscoes in 2012 (Bloater, see Lake Ontario description) and 2018 (Cisco in Saginaw Bay, see Lake Huron description). Over this same time, managers in Lake Erie and Lake Michigan sought more information about the feasibility of restoring Cisco, but no formal restoration programs were undertaken. These differences in restoration actions among lakes are a consequence of having multiple management jurisdictions that have differences in their priorities. As a result, rather than seeking to implement some basin-wide coregonine restoration action, several organizations under the aegis of the GLFC sought to develop a science-based, basin-wide multi-jurisdictional *framework* that could be applied at the lake level to respond to the conditions and uniqueness of each lake and connecting channel while also seeking to address the priorities of the fishery management agencies. Such a framework also provided the potential to transfer lessons learned from the ongoing efforts and likely has been helpful in securing federal funding from the US Environmental Protection Agency (EPA) and their Great Lakes Restoration Initiative (GLRI).

The first basin-wide, dedicated symposium on the topic of coregonine restoration occurred at a GLFC-sponsored workshop in Sault Ste. Marie, ON, in December 2016. Although no proceedings were published, a summary of the meeting can be provided by John Dettmers (GLFC). By the following spring, at an 20 April 2017 meeting, the CLC reached consensus to "*encourage individual lake committees to, where appropriate, foster a resilient coregonine assemblage as part of the prey fish community that supports diverse fisheries in a changing ecosystem*" (Steve LaPan, New York State Department of Environmental Conservation (retired), Chair of the CLC, personal communication, 5 April 2023). Similarly, the Committee of Advisors to the GLFC, consisting of US and Canadian representatives from key stakeholder groups, passed a resolution in 2017 urging "*… all fishery management agencies to prioritize coregonid restoration and develop a Great Lakes-wide strategy to determine the species or forms of coregonines of greatest relevance to each lake, ensuring the best available science is utilized*" (Available from http://www.glfc.org/pubs/pdfs/resol2017_4.pdf).

Forging consensus on complex natural-resource challenges like a native fish restoration strategy is difficult, even in small ecosystems with limited jurisdictions. Finding a cooperative way forward across the Great Lakes, which have a combined surface area of more than 244 000 km^2 and include more than 13 jurisdictions with management authority, would not have been possible without the JSP process hosting regularly structured science and management meetings at the lake and basin scales. After two years of discussion on the topic of a science-based, basin-wide framework, consensus was reached on 1 May 2018, when the CLC endorsed the CRF (Fig. 2; Brian Locke, Ontario Ministry of Natural Resources and Forestry, Chair of the Council of Lake Committees, personal communication, 13 April 2023), which, in turn, set in motion a series of tangible actions, timelines, and reporting expectations (described below under subsection "Implementing").

Describing the Coregonine Restoration Framework

Foundational principles

The CRF is founded on several well-established principles in conservation biology and resource management. The first one is the adaptive management approach, which has a long history in natural resource management (e.g., Holling 1978; Walters 1986; Williams et al. 2007). Briefly, the concept seeks to reduce uncertainty in how management actions will influence target populations toward an objective that was informed by stakeholder input. Through an iterative process, an adaptive management approach seeks to learn from the implementation of management actions, some of which could be considered experimental (Walters and Holling 1990). With the knowledge gained through monitoring a management action, strategies can be adapted to reflect new knowledge and, ideally, improved understanding of a conceptual or mathematical model that represents the ecosystem. In the CRF, the jurisdictions with management authority are considered the key stakeholders that set the priorities and objectives in the adaptive management process while also providing cross-jurisdictional oversight of the restoration implementation. The planning phase of the CRF will identify sources of uncertainty and develop models that represent our understanding of the processes that govern the dynamics of targeted species or forms [e.g., habitat models, threats' assessments, and population viability analysis (herein, PVA)]. It will take many years to implement management actions to restore species and their habitats and properly evaluate, adjust, and realize objectives. As such, the overall adaptive process will likely be multi-decadal.

A second foundational principle is the "three Rs (resiliency, redundancy, representation)," which are key dimensions by which conservation success can be measured (Shaffer and Stein 2000) and that have been applied by federal and international agencies to assess species recovery (e.g., Wolf et al. 2015; Akçakaya et al. 2018). Shaffer and Stein (2000) used the term "resiliency" to describe the characteristic of a population being able to recover from a disturbance. Resiliency is a nondecreasing function of population abundance and intrinsic growth rate; increases in abundance and growth rate cause increases in resiliency to a point where it, in theory, levels off. Some events are so severe and catastrophic (e.g., oil spill, disease, and invasive species), however, that they can overwhelm the resiliency of a population. To that end, Shaffer and Stein (2000) used the term "redundancy" to describe the extent to which the distribution of a species serves to "spread the risk" from severe impacts that may jeopardize its persistence. High redundancy, either through having multiple resilient populations or a widely distributed population that encompasses areas of low and high risk, can provide refugia and sources for recolonization and recovery after catastrophic events. In theory, the risk of extirpation decreases rapidly with increases in redundancy. Not all disturbances are temporary, however, and some lead to long-term change. Conserving a species within the breadth of environments where it was known to occur can also serve as proxy for genetic diversity. Shaffer and Stein (2000) used the term "representation" for restoring a species to the full diversity of environments where it was known to have occurred to conserve evolutionary or even cultural value. Hence, when restoration plans are drafted within the CRF, these three key dimensions (i.e., three R's) could be considered to maximize the chances of long-term restoration success.

A third foundational principle is that habitat complexity can support and(or) give rise to diversity, both within and among species (e.g., MacArthur 1965; Tews et al. 2004). Complex habitats likely provide ecological opportunity when colonized, which can drive adaptive radiations (Rainey and Travisano 1998; Yoder et al. 2010; Skúlason et al. 2019) or the creation of ecomorphs when frequent dispersal and introgression can prevent speciation (McKay and Zink 2015). In addition to supporting among-species diversity and potentially driving ecological diversification over time, complex habitats can also promote spatial structuring of populations within a species. For example, in fishes, a multitude of different spawning habitat types coupled with some degree of spawning-site fidelity can lead to population structuring and divergence (e.g., Hendry et al. 2000; McGlauflin et al. 2011). Among European coregonines, sympatric speciation likely resulted from reproductive isolation in space (different depths) and time (Vonlanthen et al. 2009, 2012). Finally, habitat complexity in and of itself can support ecosystem functional diversity (Alsterberg et al. 2017). As such, conserving and restoring complex habitats can be key for maintaining biodiversity and promoting community and ecosystem productivity, resilience, stability, and sustainability.

A final foundational principle underlying the CRF is the portfolio concept. This principle is analogous to probability theory that informs investment portfolios: diversifying assets stabilizes returns. In a biological context, the dynamics of the ecosystem are less volatile than those of its individual species; thus, biocomplexity (i.e., within- or among-species diversity) provides stabilizing effects across gradients of proximate and underlying threats (Schindler et al. 2010, 2015). For example, Hilborn et al. (2003) found that the stability and sustainability of the sockeye salmon (*Oncorhynchus nerka*) fishery in Alaska's Bristol Bay could be attributed to different riverine populations performing well at different times over the past century. Without the contributions of multiple populations variably increasing or decreasing with environmental regime shifts, the decline of a previously abundant population could have resulted in substantial impacts to the overall stability of the fishery. An additional asset of diversified prey portfolios is more consistent access to food resources for predators (Schindler et al. 2010). Conversely, less diverse portfolios lead to reduced resistance to perturbation and reduced resilience, ultimately affecting the adaptive capacity of the ecosystem (McMeans et al. 2016). In the Great Lakes, reduced production from riverine stocks of Lake Erie Walleye (*Sander vitreus*) in recent decades has resulted in a single open-lake reef stock dominating larval production and generating suboptimal portfolio effects as compared to the potential buffering capacity of the historical population structure, which included multiple large adfluvial populations (DuFour et al. 2015). Hence for ecosystems such as the Great Lakes that have undergone numerous anthropogenic disturbances, restoring and maintaining a healthy portfolio of coregonine diversity, perhaps by concomitantly seeking to maximize habitat complexity, could increase ecosystem stability and resiliency.

Planning

During the development of the CRF, four key planning areas were identified to inform the drafting and implementation of a restoration plan. An underlying philosophy of this planning is that it will be based on the best available information, ideally synthesized, recognizing the urgency to act before existing diversity or distributions are further reduced. New data and discoveries will still be important and can still be incorporated within the adaptive framework. Below, we provide more details on these planning steps (see orange boxes in the upper right of Fig. 2).

Resolve coregonine taxonomy using genetics and ecology

A critical component of conservation and restoration planning is the ability to describe and partition animals into units that reflect evolutionarily significant biodiversity (Ryder 1986; Coates et al. 2018). Units can be organized spatially and are commonly based on some level of taxonomic resolution, but they do not require complete resolution of the taxonomy. Because coregonines display an extensive array of phenotypic and ecological variation that lends uncertainty to taxonomic designations (Svärdson 1949), delineating specific and subspecific diversity has been historically challenging in the Great Lakes. Koelz (1929) first described the taxonomy of coregonines of the Great Lakes by identifying key morphological characteristics, bathymetric distributions, and reproductive characteristics. The addition of mitochondrial and microsatellite analyses of North American ciscoes indicated that variation in these loci reflected geography, rather than taxonomy, including among members of the cisco species complex in the Great Lakes, causing Turgeon and Bernatchez (2003) to recommended that a single taxon *C. artedi* (sensu lato) be recognized. When Eshenroder et al. (2016) synthesized contemporary and historical morphological data on ciscoes of the Great Lakes and Lake Nipigon, the authors used the names of species out of convenience while also recommending that members of the species complex be relegated from species to "forms," following Turgeon and Bernatchez (2003). Since then, however, genomic data have consistently detected discrete differentiation among Cisco and several extant deepwater ciscoes in the Great Lakes (e.g., Ackiss et al. 2020; Lachance et al. 2021; Bernal et al. 2022). Vast environmental and ecological changes have occurred in the Great Lakes since the standing taxonomic assignments were established by Koelz (1929), and research using both museum specimens in the collections at the University of Michigan (Ann Arbor, MI) and the Royal Ontario Museum (Toronto, ON) and extensive scale archives dating back to the early 20th century at the USGS Great Lakes Science Center could be used to compare historical and contemporary morphological and genomic diversity. This type of work is particularly relevant since hybrids among the major putative species in Lake Superior have been documented (Ackiss et al. 2020; Lachance et al. 2021), and differences between historical and contemporary morphological traits in ciscoes in Lake Huron have been hypothesized to be the result of introgressive hybridization (Todd and Stedman 1989; Eshenroder et al. 2016). Introgression has been documented in European whitefishes, where substantial environmental degradation led to the breakdown of reproductive isolation and speciation reversal in alpine lakes (Vonlanthen et al. 2012; Frei et al. 2022). Evaluating the relative roles that rapid adaptive change and hybridization-mediated change have played in documented morphological shifts will be important to inform how dynamic the taxonomic relationships in Great Lakes ciscoes have been over the past century.

Given the emergence of new morphological and genetic information over the past decade, re-evaluating taxonomic relationships was identified as one of the primary objectives during the planning phase of the CRF. To begin this process, a taxonomic review of ciscoes in the Great Lakes and Lake Nipigon was undertaken in May 2022 by the Joint Committee on the Names of Fishes Committee of the American Fisheries Society and American Society of Ichthyologists and Herpetologists (N. Mandrak, personal communication, 24 March 2023). Because we expect to continue to advance knowledge in genetics, morphology, and ecology (including hybridization), taxonomic revision in ciscoes is viewed as an ongoing process that can be updated with new data rather than the occurrence of a single, fixed decision.

The second primary objective of this component of the CRF is to delineate spatial units for the conservation, restoration, or management of cisco diversity across the Great Lakes Basin, independent of higher-order taxonomic decisions. A novel methodology that can delineate spatial units at appropriate resolution for threats assessments or PVA has been developed. Briefly, it includes an empirical process that merges principles of both conservation and restoration ecology (e.g., Waples 1991; Moritz 1994; Waples 1995; Crandall et al. 2000; Fraser and Bernatchez 2001; Wood and Gross 2008; COSEWIC 2020) and includes management opportunities for enhancing ecosystem services (Luck et al. 2003). This method establishes three categories of spatial units: (1) "occupied" units defined by evidence of reproductive isolation or evolutionary significant diversity, which are similar to the well-established concepts of conservation units, including evolutionary significant units (Waples 1991, 1995) associated with the ESA and designatable units used by COSEWIC (2004); (2) "unoccupied" units that represent restoration opportunities associated with extirpated biodiversity given that the space was historically occupied but is now locally extirpated; and (3) "service" units that represent space that has low or no probability of being historically occupied (nor is currently occupied) but could be considered for management to provision desired ecosystem services (sensu Luck et al. 2003) for cultural, functional, or economic benefits. Assessing Indigenous knowledge and data that provide evidence for the validity of specific criteria can be used to delineate each unit type. A spatial characterization of coregonine units could provide managers with a tool to assist in making conservation, restoration, and strategic management decisions.

Gap analysis: describe and map historical and contemporary populations and habitats

Analysis of historical data plays a vital role in conservation and restoration ecology (Alexander et al. 2009; Szabó 2010; Pooley 2018). Spatial analysis of historical data can illustrate where critical habitat once existed and where losses have occurred, show distributional shifts, and help target or inform contemporary restoration options (Tingley and Beissinger 2009; Ferrer-Paris et al. 2014). Inventorying historical and contemporary coregonine habitat use and distributions across the Great Lakes is a foundational planning step in the CRF. This effort will occur in three parts: data curation, mapping and modeling suitable and occupied habitat, and identifying gaps, which could represent conservation or restoration opportunities based on historical and contemporary habitat use. Although habitat used at all life stages could potentially be important to identify, conserve, or restore, spawning habitat will be the first focus given its general importance in many other aquatic conservation and restoration efforts (e.g., Taylor et al. 2019). Lack of spawning habitat can limit recruitment and population abundance (Rosenfeld and Hatfield 2006) and has been identified as a potentially limiting factor in Cisco rehabilitation (Madenjian et al. 2011).

Rich and diverse records of coregonine occurrence and habitat conditions are housed in libraries, archives, and online catalogues across the Great Lakes basin. Historical data include targeted fishery independent surveys, fisheries catch data, published reports that summarize surveys and oral histories (e.g., Organ et al. 1979; Coberly and Horrall 1980; Goodyear et al. 1982), photographs, Indigenous knowledge (Duncan et al. 2023), and museum specimens. Contemporary coregonine distributions have been recorded through regular standardized survey programs across agencies since the late 1970s (e.g., Bunnell et al. 2006; Gorman 2012; Weidel et al. 2022), and telemetry-derived data are becoming available (see https://glatos.glos.us/). Data from these sources are being gathered, digitized, and databased (C. Brant, unpublished data). Importantly, data curation can make these data accessible (machine readable) and mappable, thereby ensuring useability for CRF and future research. Curated data, as well as existing databases, could be used for mapping, modeling, and evaluating species and habitat distributions.

Species distribution models (SDMs) can be used to describe relationships between species observations and habitat characteristics and to generate predictive maps of the probability of a species occurrence, even in locations with no sampling data. SDM approaches (reviewed in Guisan et al. 2017)

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can vary with applications, scale, and data quality and quantity and are often based in regression (e.g., general linear or additive models) or machine learning (e.g., Boosted Regression Trees or Maxent). Within the CRF, starting with basin-wide models could highlight regions that would benefit from further work to address management needs with models of smaller extents, finer scales, and where high-quality data are available. Finally, comparing mapped and modeled habitat use and occurrence across historical and contemporary periods can inform decision-making related to restoration. One direct and immediate application is that the distributions generated through this process could be used to inform the delineation of spatial units, as described above. For example, if a species was historically present in a certain area but now absent despite apparent suitable habitat, managers could choose to prioritize this "unoccupied" spatial unit for restoration.

Compile data to conduct population viability

Restoration or conservation of coregonines within the CRF could involve deciding among a myriad of management actions that have the potential to reverse ongoing declines or improve long-term sustainability of populations. However, identifying which actions are most likely to benefit coregonines is daunting, given the uncertainty in population structures, distributions, and the many factors influencing population dynamics. Population models provide a tool to aid this decision-making, allowing managers to explore the consequences of actions before they are implemented and to test prior beliefs about how the natural system operates (Starfield and Bleloch 1991).

PVA seeks to evaluate species-, location-, and time-specific criteria for population persistence (Soulé 1987). The umbrella of PVA includes a variety of qualitative or quantitative analyses to predict the future status of a population or a collection of populations (Morris and Doak 2002), and PVA can play a significant role in recovery planning (e.g., Morris et al. 2002). A common attribute of PVA is the inclusion of stochastic (random) effects so that abundance at any time is represented by a probability distribution rather than a single, deterministic value (Sweka and Wainwright 2014).

Most PVA can be classified into two general types: unstructured and structured. Both types provide useful information, but choosing which to apply depends on the question asked, prior knowledge of the species, and data availability. Unstructured PVA represents the simplest class and is based on a time series of abundance (or relative abundance) data used to evaluate a trend. It can estimate a population growth rate and project that trend into the future with uncertainty to determine a probability of extinction or quasi-extinction at some point in the future (e.g., Dennis et al. 1991). Unstructured PVA can inform a resource manager about the current status of a population and the likelihood of persistence assuming that the conditions under which the population growth rate was estimated will continue into the future. Within the CRF, an unstructured PVA can help identify coregonine populations in need of management intervention for their continued persistence (e.g., some occupied units may require conservation). Alternatively, structured PVA is more complex and incorporates mechanisms governing the population dynamics of a species such as age- or stage-specific life-history parameters (age- or stage-structured models), metapopulation dynamics (metapopulation models), or attributes of individuals on the landscape (spatially explicit models) (Lande et al. 2003). A structured PVA allows managers to test hypotheses about the factors influencing population dynamics and investigate the potential benefit of management alternatives prior to large investments of resources.

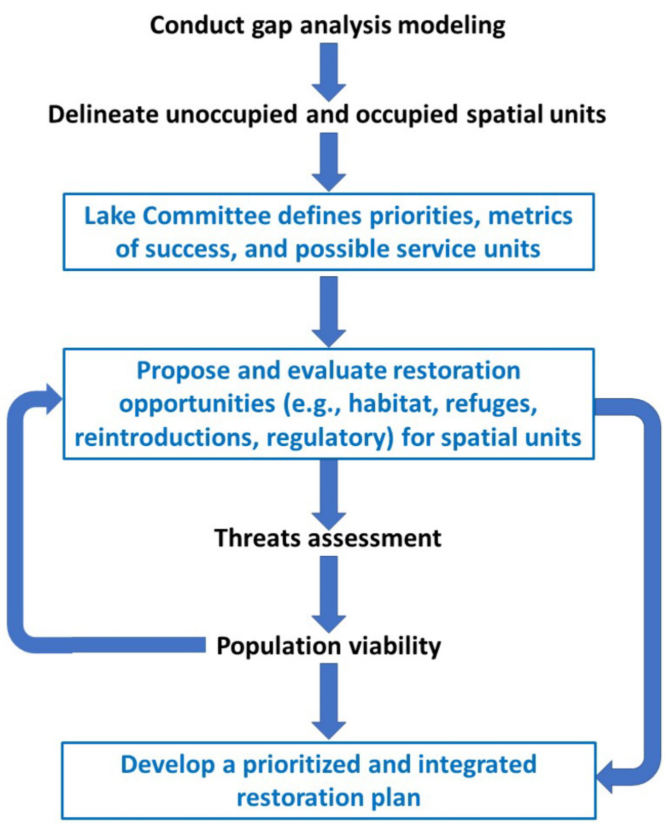
Given that data availability can influence which type of PVA can be developed, a compilation of the types of fisheries monitoring data that could provide time series of relative abundance for ciscoes and whitefishes across the Great Lakes have been recently compiled (B. Weidel, personal communication, 24 March 2023). Geneticists are also exploring the feasibility of applying close-kin mark–recapture (e.g., Bravington et al. 2016) as an alternative method to estimate abundance for some species that are rarely encountered by current monitoring efforts. Likewise, a compilation of coregonine life-history parameters (e.g., growth, age at maturity, fecundity, and annual mortality) through a review of the peer-reviewed and gray literature has been completed to help develop structured PVA models (B. Weidel, personal communication, 24 March 2023). These efforts to synthesize relevant coregonine surveys and life-history parameters could help determine which specific PVA can be implemented across the Great Lakes and could help identify where additional research or assessment is needed to fill information gaps.

Threats assessment: for extant and extirpated populations

In the context of restoration, a threats assessment identifies extrinsic factors (e.g., development, overfishing, and invasive species) that have caused, are causing, or may cause populations within a delineated spatial unit to decline in distribution, abundance, or ecological function. When threats' assessments occur for multiple spatial units across the watershed, one can determine the extent to which threats are overlapping. Threats' assessments typically account for the timing, extent, and severity of identified threats and often use a matrix combining the impact of a given threat with its extent or likelihood of occurrence to evaluate risk (Fisheries and Oceans Canada 2014; CMP 2020). A causal explanation of how threats influence populations is an important component of a complete assessment (Smith et al. 2018). Actions designed to mitigate threats, when possible, can be critical to conservation and restoration efforts and can be included in PVA (described above) to predict viability under various threat and conservation scenarios.

For the CRF, multiple threats' assessment frameworks were considered to determine which one, or combinations therein, would be best suited for application to Great Lakes coregonines. Through an iterative process, a framework based largely on the one used by Fisheries and Oceans Canada (2014) but that includes additional elements (e.g., a concep-

Fig. 3. Summary of iterative steps within the Coregonine Restoration Framework by which planning methods, once vetted through the Joint Strategic Plan process, could be used by fishery managers to develop a prioritized and integrated restoration plan. Steps without a box around the text reflect those related to planning.



tual modeling exercise to explicitly link threats to specific coregonine vital rates and(or) life stages) was recommended as the most appropriate. An important point is that while spatial unit delineation and gap analysis will focus on reproductive habitat, both PVA and threats' assessment may consider habitats supporting the whole life cycle. To finalize the threats' assessment method, practice runs using data-rich and data-poor examples from different Great Lakes species were used to determine whether additional elements should be added or existing elements be edited to improve its usage (A. Honsey, personal communication, 23 March 2023).

Restore

The CRF describes three steps in the lower right "restore" region of the framework (green boxes, Fig. 2) that are dependent on several key planning steps. Although the CRF indicates a simple linear progression of steps, the process that would lead to an integrated restoration plan could be iterative between elements of the planning and restore regions (see Fig. 3). For example, informed by the gap analysis modeling, spatial units could first be delineated for "occupied" and "unoccupied" types across the basin for relevant coregonine species. A resultant map of these units could allow managers to envision relevant scales at which conservation or restoration could occur while also highlighting areas where they could delineate "service" units. The first "restore" step in the CRF is to evaluate restoration opportunities within relevant spatial units under consideration for restoration. Multiple opportunities could be considered, including restoring or connecting habitats, undertaking reintroductions or translocations, or using regulatory authorities to create refuges or otherwise limit fishing mortality, and are described in more detail in the subsequent paragraphs.

With regard to the opportunity of "habitat and refugia," CLC (2016) already recognizes that diverse and functional habitats give rise to sustainable fish production, and that the protection and improvement of these habitats should occur systematically, adaptively, cumulatively, and collaboratively. To that end, each lake committee has recently undertaken an inventory and assessment of functional habitats, identified existing habitat-based impediments to fish production, and prioritized which habitats or environments could be ameliorated to reduce these impediments and enhance production (Jeff Tyson, GLFC, personal communication, 23 March 2023). Hence protecting or restoring habitat for coregonine restoration may be complementary to other efforts targeting other taxa. As an example of potential key functional habitat for coregonines, analyses of fishery-dependent (Baldwin et al. 2009) and fishery-independent data (Kao et al. 2020) highlighted the historical importance of embayments to Cisco, such as Green Bay in Lake Michigan or Saginaw Bay in Lake Huron. These habitats have endured anthropogenic stressors, including eutrophication and sedimentation, that could have affected the quality of habitat for spawning and embryo incubation. For example, insufficient oxygen concentrations appear to still be problematic for eggs incubating under the ice within inner Saginaw Bay (Kalejs et al. 2022). In Green Bay, however, oxygen concentrations no longer appear to be an impediment (Madenjian et al. 2011). Interestingly, the contemporary abundance of recovering Cisco in Lake Ontario is relatively high in Chaumont Bay, Lake Ontario (Weidel et al. 2021*a*), despite limited availability of interstitial spaces that are assumed to enhance embryo survival and increase recruitment potential. An increased emphasis on describing the within-species diversity of spawning habitat usage across Great Lakes Ciscoes (e.g., Paufve et al. 2021) and how egg deposition and larval emergence vary across habitats could prove invaluable to the adaptive nature of the CRF as restoration planners consider how habitat remediation fits within the suite of restoration tools.

Refuges or reserves have proven useful to conserve or even increase abundance of fish stocks in regions where recruitment overfishing is occurring and where regulations can be enforced (Hilborn et al. 2004). In the Great Lakes, fishery managers created refuges for lake trout in Lake Michigan (Holey et al. 1995) and Lake Superior (Swanson and Swedberg 1980) that were credited with promoting increases in biomass (Schram et al. 1995; Johnson et al. 2015b; Kornis et al. 2019). No such protection has ever been created for coregonines in the Great Lakes, but it has been suggested as possible (Zuccarino-Crowe et al. 2016). One potential opportunity for coregonines is the Lake Superior National Marine Conservation Area in ON, Canada, which was established in 2015 as one of the largest freshwater protected areas in the world (more than 10 000 km^2). Its interim management plan, however, only explicitly protects habitat for brook trout (*Salvelinus fontinalis*) while otherwise zoning other areas for "ecologically sustainable use" (Parks Canada 2016) and noting a "low" desire to implement a no-take or closed fishing area for any species. Recent Lake Superior surveys, however, have revealed some deepwater ciscoes such as Shortjaw Cisco to be relatively low in abundance (e.g., Bronte et al. 2010; Pratt and Chong 2012), suggesting some potential benefit from a fishing refuge. Whether or not fishing is identified to be a threat for some coregonine species in some lakes could be identified through a threats assessment or PVA in the planning stages of the CRF. Although there may be broad consensus that overfishing contributed to the local extirpation and even extinction of some coregonine species during the 20th century (e.g., Smith 1968; Christie 1974), we are not aware of clear quantitative evidence that any cisco species has been overfished in the Great Lakes in the 2000s, although evaluations have been undertaken in Lake Superior (e.g., Fisch et al. 2019).

For populations that are extirpated or have undergone declines in their distribution or abundance, stocking of artificially propagated animals or transplantation of wild animals are other restoration options, assuming suitable sources exist and any historical threats are deemed to no longer be impediments. Hatchery rearing of coregonines is routinely successful in Europe and North America (see Wanzenböck 2021), including the recent success of rearing deepwater *C. hoyi* in the Great Lakes (Holey et al. 2021). As with most stocking programs, one of the first considerations is the extent to which hatchery-reared animals could hybridize and introgress with congeners in the recipient lake given that it has been documented to occur among coregonines in European Lakes (Winkler et al. 2010; Kahilainen et al. 2011; Anneville et al. 2015). In a similar vein, it is conceivable that the introduced animals could ultimately diverge from their donor stocks. For example, the introduction of only 90 000 larval vendace *C. albula* into a Norwegian lake ultimately led to strong genetic divergence from the source population nearly a century later, likely arising from different environmental conditions (Vuorinen et al. 1991). In contrast, when Cisco from Lake Superior were stocked into several inland Minnesota lakes, they largely retained their genetic diversity and ecological niche after nearly a century, with only small shifts in morphology that were interpreted as a greater tendency toward benthivory (Jacobson et al. 2018). Whether a species reintroduced through hatchery propagation will differ from its source population may be difficult to predict, but adherence to conservation-oriented propagation practices (e.g., Flagg and Nash 1999) could maximize the probability of at least initially maintaining the genetic diversity of its source population. Beyond genetics, another consideration for using hatchery-reared ciscoes is the tendency for the animals to be "pugheaded," which is a common morphological artifact of hatchery rearing for many fish species (Näslund and Jawad 2022) and that occurs among ciscoes reared in labs and hatcheries in the Great Lakes (e.g., Todd et al. 1981). Whether this malformation in the head reduces growth, survival, or reproduction among stocked coregonines remains unknown. Finally, recent simulations that consider the size of the Great Lakes and the intermediate trophic level of some coregonines illustrate the need to concentrate reintroductions into targeted regions, given the limited capacity of fish hatcheries (Rook et al. 2022).

A second reintroduction tool for consideration is fish translocation, which we define as direct transfer of any life stage, from fertilized eggs to adults, from one lake to another. Among coregonines, evidence of translocation success was reported for European whitefish *C. lavaretus* in Scotland, whose native distribution was limited to only two lakes (Crotti et al. 2021). Over the course of 30 years, several different life stages (including adults) of *C. lavaretus* were translocated to create stocks in new lakes and reduce the risk of extirpation (Adams et al. 2014). Although some of these new populations became self-sustaining, they did exhibit some differences from their source populations with respect to morphology and diet and also exhibited reduced genetic diversity (Crotti et al. 2021; Praebel et al. 2021). A second translocation example occurred when "dwarf" Cisco from an inland Minnesota lake were transferred into three other lakes that had no coregonine populations (Shields and Underhill 1993). The animals survived and grew beyond the "dwarf" sizes that were observed in their source lake, but they never reproduced, perhaps owing to the absence of suitable spawning habitat. To our knowledge, translocation of coregonines among the Great Lakes has not been undertaken as a conservation or restoration tool, although it has been proposed but not yet undertaken for lake trout (Bronte et al. 2008). Although translocation potentially carries the same risk to reduce genetic diversity as can occur through hatchery propagation, it has been documented to be an effective conservation tool elsewhere with other species (e.g., Minckley 1995; Olden et al. 2011; Yackulic et al. 2021). Translocation of adult deepwater ciscoes may prove difficult in the Great Lakes, given these fish are generally caught in deeper waters (>50 m) and are vulnerable to severe barotrauma (Gorman and Keyler 2016). Translocation of younger life stages that can occupy shallower water would still have to overcome the sensitivity to capture and handling and the threat of pathogen or parasite transmission.

The final two steps of "restore" could involve fishery managers developing and implementing a prioritized and integrated restoration plan. To determine which opportunities or suite of opportunities would be prioritized, a threats' assessment of extrinsic factors could be undertaken at the relevant spatial scales under consideration for restoration. For example, identification of degraded spawning habitat as a threat would logically favor implementation of a different restoration tool than if overfishing were identified as a threat. Likewise, a structured PVA could provide additional quantitative evidence for the effectiveness of different restoration tools. We anticipate that conducting threats' assessments and PVA (which can include simulating multiple restoration opportunities) through an iterative process with fishery managers could foster the development of this prioritized and integrated restoration plan and help ensure that the foundational principles of the CRF are incorporated (Fig. 3). At the same time, we acknowledge that the detailed process of how the restoration plan could be achieved would be enhanced through learning from our initial experience.

Evaluate and learn

A key component of the adaptive management approach is evaluation of the "restore" action, i.e., the left half (blue boxes) of the CRF (Fig. 2). The first two steps include the monitoring of fishes (i.e., populations) or key habitats that have either been improved or created (e.g., refuges, improved spawning habitat, and removal of dams). Monitoring would consist of using existing surveys and designing new surveys targeting multiple life stages of fishes or multiple aspects of fish habitat (e.g., substrate, oxygen, flow, and density of invasive mussels). The third step is to aggregate or synthesize the data across spatial units, if necessary, followed by the important fourth step of reporting the evaluation results to the lake committee. The final step is to update the conceptual or mathematical models to reflect our understanding of the species and their habitats within the ecosystem, which is a key component of the adaptive management approach.

Implementing the Coregonine Restoration framework

As previously stated, the CLC endorsed the CRF as a basin-wide, science-based approach to Great Lakes coregonine restoration in May 2018. Since that time, several important efforts (described below) have been undertaken in anticipation of a lake committee initiating a new coregonine restoration effort that could execute the framework from its initial planning stages. It is important to acknowledge, however, that the adaptive nature of the CRF allows for existing restoration efforts on Lake Ontario and Saginaw Bay, Lake Huron, to be fully accommodated in the "Evaluate and Learn" steps.

The first important effort to begin implementation was the CLC endorsing a process for the planning steps of the CRF on 23 April 2019 (Brian Locke, Ontario Ministry of Natural Resources and Forestry, Chair of the Council of Lake Committees, personal communication, 13 April 2023). Specifically, CLC recommended that a multi-agency team, comprised primarily of JSP agencies but also supplemented by experts from academics or other organizations, be formed for each of the four planning boxes. These teams were charged with developing methodologies for each box and vetting them through the JSP process (i.e., through the lake technical committees and CLC). By 2021, all four teams had been formed and included 53 individuals spanning 21 entities (e.g., state, provincial, and federal agencies, U.S. Tribes, Canadian First Nation, non-profit organizations, and universities) based in Canada and the US. All five proposed methodologies have now been approved by the CLC (J. Dettmers, personal communication, 21 April 2023).

Investment in resources was also required to implement the CRF following its endorsement by the CLC, and several Great Lakes agencies have stepped forward. First, the U.S. EPA-GLRI has supported coregonine restoration in multiple ways (see https://www.glri.us/projects). For example, a steering committee comprising members of U.S. federal agencies has made recommendations to fund more than $6.8 million USD across 51 annual projects over 6 years focusing on planning efforts, operational support of existing restoration efforts in Lake Ontario and Saginaw Bay, Lake Huron, and monitoring of these restoration efforts (Kurt Schilling, USFWS and Co-Chair, personal communication, 27 March 2023). Another important investment occurred in 2022 when GLRI began making annual $1.85 million USD investments toward new multi-agency, experimental research to support the CRF at the USGS Tunison Field Station in Cortland, NY. Secondly, beginning in 2019, the GLFC funded three new coregonine science positions at USGS to increase research capacity in the basin (A. Muir, personal communication, 24 March 2023). Likewise, GLFC has an annual request for proposals targeting native fish restoration, partially supported through GLRI, which has included coregonine projects (http://www.glfc.org/science-research.php). Finally, since 2019, USFWS has invested $10.3 million USD in base funding to support coregonine research and operations (Kurt Schilling, USFWS, Fisheries Information System, 27 March 2023). This recent influx of funding dollars to support new scientists and research, assessment activities, and hatchery rearing capacity has been critical to operationalizing the CRF.

Maintaining and enhancing support from stakeholders (e.g., recreational anglers and commercial fishers) and the broader public could be cultivated to help ensure that recent investments can be sustained and that fishery managers will have sufficient support to initiate or maintain restoration efforts. To that end, a website could be developed to increase public awareness of coregonine restoration and improve coordination among those already engaged. Given the cultural and economical importance of coregonines to Indigenous communities in the US and Canada, even greater engagement from Tribes and First Nations could be prioritized. Although stakeholder support, including the statement from the GLFC Advisors in 2017, may have facilitated endorsement of the CRF by the CLC in 2018, newer efforts to engage stakeholders and the public could be required given the diversity of resource management needs that exist across the Great Lakes.

A final key aspect of implementing the CRF has been to enhance coordination of the coregonine efforts across the Great Lakes basin and to learn from other native fish restoration efforts. One successful effort to improve coordination was the creation of a GLFC-sponsored monthly Coregonine Science webinar series in April 2021 that has averaged more than 75 attendees per session to date (as estimated by Zoom software). The webinar topics have been diverse, including science topics about coregonine ecology and evolution, operational topics regarding the challenges of hatchery rearing, and monitoring topics about the ongoing efforts in Lake Ontario and Saginaw Bay, Lake Huron (contact D. Bunnell for more information). We have also sought to learn more broadly about coregonine research in other systems by inviting speakers to describe their work outside of the Great Lakes basin (e.g., Alaska, Finland, France, Ireland, and Switzerland). To determine key "lessons learned" from previous native fish restoration efforts in lakes across North America, we sponsored a symposium at the 151st annual meeting of the American

Fisheries Society in 2021 (see https://afsannualmeeting2021.fisheries.org/preliminary-list-of-symposia/). Continued learning and assimilation of scientific and social information from other large-scale fishery and habitat restoration strategies could help us maintain and grow long-term interest and support across large and diverse geographies, adapt and capitalize options and solutions to address large-scale complex natural resources obstacles, and maintain programmatic and governance efficiencies. Future coordination goals within the Great Lakes basin could include developing an annual or biennial symposium where we could bring biologists, fish culturists, and fishery managers together to discuss progress and next steps of the CRF. We envision sharing presentations and posters to disseminate research efforts and best practices, as well as facilitating discussions on a variety of possible topics, including defining restoration priorities and metrics of success, prioritizing key knowledge gaps, or brainstorming ideal sampling methods to improve monitoring of coregonines at specific life stages.

Conclusion

The Great Lakes were once home to a diverse community of coregonines that thrived in connected habitats, including free-flowing rivers and a complex mix of shallow and deepwater habitats. Today, only a fraction of the historical coregonine diversity has persisted, primarily in Lake Superior, and habitats have been stressed or disconnected to some extent across each of the Great Lakes (Allan et al. 2013). Despite these losses, there are currently no active and legally mandated efforts (e.g., driven by SARA or ESA) to conserve existing coregonine diversity or address important habitat challenges. Likewise, restoration of locally extirpated species goes beyond the scope of federal conservation laws. For this reason, fisheries managers have undertaken their own restoration efforts in Lake Ontario and Lake Huron and have since endorsed the CRF to guide future efforts that will likely arise in other lakes. Restoring coregonines and their habitats in the Great Lakes will certainly require long-term commitments and persistence and likely some trial and error, given that other Great Lakes native fish restoration efforts have taken several decades with mixed success. Lake Trout restoration, for example, was successful within about two decades in Lake Superior but has yet to produce self-sustaining wild populations in some lakes, including Lake Ontario and Lake Erie despite large hatchery stocking efforts (i.e., 55 million fish stocked in Lake Ontario since 1973 and 11 million fish stocked in Lake Erie since 1978; USFWS/GLFC Great Lakes Stocking database: http://fsis.glfc.org/). Given that lake trout are a top predator and can attain a larger size in their first three years of life [e.g., ∼400 mm (He and Bence 2007)] than coregonines [Bloater ∼200 mm (Bunnell et al. 2012); Cisco ∼275 mm (Stockwell et al. 2009)] and thereby likely have a reduced risk of predation, restoring coregonines could prove more challenging than restoring lake trout given the extensive predator community that exists in many lakes. Other relatively new threats to coregonines have arisen in recent decades, including a changing climate and expanding dreissenid mussels, concomitant with declining *Diporeia* spp. in all lakes but Superior. These challenges should reinforce urgency while seeking to balance the need for careful planning to maximize the likelihood of success with resources that will always be limited due to the size of the Great Lakes. Despite these challenges, there are reasons to be hopeful. Long-term efforts have led to improvements in water quality, restoration of some habitats, control of sea lamprey, and the establishment of the JSP, which greatly diminishes the likelihood of future overfishing. These achievements have set the stage for native coregonines to have a greater likelihood of restoration success today compared to earlier decades. Ideally, the CRF will position Great Lakes managers and scientists to work collaboratively and efficiently toward achieving restoration targets and compensating for some of the losses of the past for the good of the ecosystem and its stakeholders.

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