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Moving repatriation efforts forward for imperilled Canadian freshwater fishes

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1 **Title:** Moving repatriation efforts forward for imperilled Canadian freshwater fishes

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3 **Authors:** Karl A. Lamothe^{1*} and D. Andrew R. Drake²

4

5 **Affiliations:** ¹Great Lakes Laboratory for Fisheries and Aquatic Sciences, Fisheries and Oceans
6 Canada, 867 Lakeshore Rd., Burlington, ON Canada L7T 3M3; karl.lamothe@dfo-mpo.gc.ca

7 ²Great Lakes Laboratory for Fisheries and Aquatic Sciences, Fisheries and Oceans Canada, 867
8 Lakeshore Rd., Burlington, ON Canada L7T 3M3; andrew.drake@dfo-mpo.gc.ca

9

10 **Corresponding author:** Lamothe, K.A.; Twitter: @KarlLamothe; ORC Id: 0000-0001-9875-
11 8204; P: 905-319-7245

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12 **Abstract**

13 Freshwater ecosystems are among the most threatened environments on our planet. Disturbances
14 across the terrestrial landscape accrue within freshwater ecosystems and, combined with global
15 stressors like climate change and invasive species, create a complex situation for recovering
16 imperilled fishes. Given the drastic global trend of freshwater fish declines, similarly extreme
17 efforts are needed for their conservation and recovery – repatriation represents one such
18 opportunity. Species repatriation describes the act of releasing a species in areas where
19 extirpation has occurred. Paradoxically, a long history of fish introductions for recreational
20 purposes exists, yet examples of repatriation for imperilled fishes are relatively rare compared to
21 terrestrial species. Stemming from the restoration and species introduction literature, we identify
22 five ecological themes to consider when evaluating repatriation potential of freshwater fishes and
23 suggest that repatriation represents the “drastic” approach needed to achieve meaningful
24 conservation milestones.

25 **Keywords:** conservation, freshwater fishes, endangered species, repatriation

26 **Introduction**

27 Species repatriation involves the intentional return or release of a species within its native
28 range at locations where it has previously been extirpated, and therefore represents one of several
29 conservation strategies for improving the status of imperilled species. Efforts to repatriate
30 species have occurred across a diverse array of taxa including plants (Godefroid et al. 2011),
31 birds (Armstrong et al. 2002), and mammals (Landa et al. 2017); however, freshwater fishes
32 have been relatively underrepresented among repatriation efforts (Seddon et al. 2005; Seddon et
33 al. 2014; Cochran-Biederman et al. 2015). Among the few Canadian freshwater fishes for which
34 repatriation has occurred, most efforts have been directed towards charismatic and
35 recreationally-important species such as Atlantic Salmon (*Salmo salar*), Westslope Cutthroat
36 Trout (*Oncorhynchus clarki lewisi*), and Lake Sturgeon (*Acipenser fulvescens*), which all have a
37 large stakeholder support group. The overall underrepresentation of fishes among conservation-
38 driven repatriation efforts is in contrast with their heightened rates of population decline,
39 conservation status, and extirpation rates (Dudgeon et al. 2006; Strayer and Dudgeon 2010; Reid
40 et al. 2018). During the 20th century, freshwater fishes had the highest extinction rates among all
41 North American vertebrates (Burkhead 2012), with approximately 65 percent of freshwater
42 fishes experiencing population declines since 1970 (Baillie et al. 2010). Despite these alarming
43 trends, biases in funding and resulting conservation momentum towards charismatic bird and
44 mammal species has likely led to the underrepresentation of fishes among repatriation initiatives
45 (Clark and May 2002; Seddon et al. 2005).

46 Adding to the paradox, humans have successfully moved freshwater fishes around the
47 globe for well over a century. The objective of most freshwater fish stocking programs is to
48 support or enhance production of populations important for recreational or commercial fishing

(Pister 2001; Malony et al. 2003). Top predators such as Smallmouth Bass (*Micropterus dolomieu*) or Rainbow Trout (*Oncorhynchus mykiss*) are often the subjects of freshwater fish stocking programs as they are among the most sought-after species for fishing purposes (Eby et al. 2006). Rarely have fish stocking programs focused on species that lack obvious recreational value, such as where the primary goal of releasing individuals is to mitigate extinction risk (but see, for example, Shute et al. 2005). This passive neglect for non-recreational species is likely driven by societal demand for aquatic ecosystems to serve as multifunctional ecosystem service providers (e.g., recreational angling, hydroelectricity, drinking water). Only within the last several decades, as conditions of freshwater ecosystems have deteriorated, and conservation legislation been established, has species conservation become an important area of interest from a species repatriation perspective.

Notably, there are many differences between introducing sport fishes and repatriating imperilled species. First, species commonly stocked in freshwaters for recreational or commercial purposes tend to have widespread geographic distributions (e.g., Rainbow Trout, Smallmouth Bass), allowing greater opportunities to understand and characterize ecological and life-history parameters (e.g., vital rates), as well as variables such as optimal stocking density. In contrast, most imperilled or extirpated fishes have geographically restricted, patchy distributions, and low population sizes, limiting our ability to understand critical life-history and ecological requirements vital for recovery. For example, Spring Cisco, an ecomorphotype of the Cisco (*Coregonus artedii*) presently listed as *Endangered* under the Canadian *Species at Risk Act* (SARA 2002; Fisheries and Oceans Canada 2014a), is found in only one lake in southwestern Québec. Along with critical uncertainties regarding the ecology of many imperilled freshwater fishes (Rosenfeld and Hatfield 2006), large uncertainties likewise exist around best-management

strategies for recovering these fishes. For example, at what point are restoration efforts deemed sufficient to begin repatriation efforts for an extirpated species? Only recently have studies begun to consider the number of propagules needed to seed a historically extirpated population (e.g., Dunham et al. 2011), whereas stocking of recreationally or commercially important species is typically limited by the number of individuals that a hatchery can produce. Given the difficulties of translocating and/or breeding endangered species in captivity (Brown and Day 2002), attaining sufficient stock sizes for repatriating species can be challenging. Finally, social constructs are an important consideration given the potential policy issues regarding the release and subsequent protection of imperilled species (Pettorelli et al. 2018) and the long-term financial commitments needed to support such an effort (Helmstedt and Possingham 2016).

In Canada, few imperilled freshwater species have been the subject of repatriation efforts for conservation purposes despite longstanding recommendations for repatriation within species recovery strategies. Here, we identify several ecological considerations for repatriation relevant for Canada's imperilled freshwater fishes based on current knowledge from restoration ecology and fish introductions. First, we describe the current state of repatriation efforts across species protected under the Canadian *Species at Risk Act* (SARA 2002). We then provide an overview of five ecological and management factors to consider prior to initiating repatriation. Overall, we hope this paper will bring increased attention to the numerous scientific gaps surrounding repatriation efforts for imperilled Canadian freshwater fishes, and in doing so, will stimulate action and scientific debate as to where, when, why, and how to initiate repatriation as part of a broader, multi-tiered species conservation program.

Repatriation of imperilled Canadian freshwater fishes

The primary objective for species repatriation is to improve the overall status of wild populations by establishing self-sustaining, breeding populations in areas where they historically resided but have been lost (George et al. 2009). We focus on the term ‘repatriation’ instead of the commonly used ‘reintroduction,’ as the latter can be confused with the act of repeatedly introducing a species (native or otherwise); species repatriation, by definition, describes the act of returning a species to its native habitat. We use the term ‘supplementation’ to describe the concept of improving wild imperilled stocks (i.e., non-extirpated) through stocking efforts. Finally, we use the term ‘translocation’ to describe the act of removing individuals of a species from one location and releasing them into a different location.

Several studies have demonstrated that freshwater fishes have been relatively underrepresented among repatriation studies. For example, Seddon et al. (2005) found that only 4% of published repatriation studies pertained to fishes despite consisting of approximately 50% of all described vertebrate species on Earth. Later, Champagnon et al. (2012) found that among 263 documented cases of restocking vertebrates, approximately 24% dealt with fishes, with the majority of studies focused on birds (40%) or mammals (27%). This apparent underrepresentation of freshwater fishes is likely reflective of research capacity, funding, and management interest for fishes compared to more charismatic taxa. However, the prevalence of species repatriation and supplementation efforts across federally protected taxa in Canada has yet to be investigated.

In Canada, federal protection for imperilled wildlife taxa is provided by the SARA (2002). To gain federal protection, Designatable Units (DUs) of species are assessed by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC), which is used to provide a recommendation to the Minister of the Environment and Climate Change as to whether

a species should be considered for protection. DUs consist of discrete, evolutionarily significant units of the taxonomic species, where evolutionary significance implies that the DU is important to the evolutionary legacy of the species as a whole, and if lost, would likely not be replaced through natural dispersal (Government of Canada 2017). Freshwater fishes comprise 66 of the 580 DUs listed as Special Concern (SC), Threatened (THR), Endangered (EN), or Extirpated (EXP) in Canada compared to 180 vascular plants, 83 birds, 48 arthropods, 43 reptiles, 39 terrestrial mammals, 29 molluscs, 28 marine mammals, 25 amphibians, 16 lichens, 15 mosses, and 13 marine fishes. Depending on SARA status, the Government of Canada produces Management Plans (SC), Recovery Strategies (THR, EN, EXP), and/or Action Plans (THR, EN, EXP), which provide information as to what measures have and should be taken to conserve or recover the species in question. To characterize the research landscape and understand whether freshwater fishes are underrepresented in repatriation initiatives, we evaluated whether efforts involving population supplementation, repatriation, or translocations have been performed for each species in the past, and whether introductions will be considered as a future strategy for conservation as defined in federal recovery strategies.

We found that freshwater fishes are relatively underrepresented among repatriation and supplementation efforts for federally listed species in Canada compared to other taxa (Figure 1). SARA-listed fish species for which introductions have occurred include Atlantic Whitefish (*Coregonus huntsmani*), Copper Redhorse (*Moxostoma hubbsi*), Striped Bass (*Morone saxatilis*), Westslope Cutthroat Trout, and White Sturgeon (*Acipenser transmontanus*). Across taxa, vascular plants had the greatest number of repatriation or supplementation efforts identified or underway followed by birds, freshwater fishes, arthropods, and reptiles (Figure 1). In proportion to the number of species listed per taxon, amphibians had the greatest proportion of repatriation,

supplementation, or translocation efforts completed (16%), followed by terrestrial mammals (15%), vascular plants (15%), freshwater fishes (12%), and molluscs (10%). Despite the low numbers of executed augmentation efforts across species, 128 Recovery Strategies, Management Plans, and/or Action Plans indicated repatriation, supplementation, or translocation as a possible recovery strategy. Among those, vascular plants had the greatest proportion (36%) of species with repatriation, supplementation, or translocation identified as a potential recovery strategy, followed by molluscs (34%), arthropods (31%), reptiles (23%), amphibians (20%), mosses (20%), and freshwater fishes (12%).

Ecological considerations for species repatriation

The first and most important factor to consider before initiating species repatriation efforts is how and why the species was originally extirpated (Armstrong and Seddon 2008; Cochran-Biederman et al. 2015). The rationale for identifying causative factors of species decline is that these factors must be reduced such that a high likelihood of successful repatriation can be achieved. Reducing causative factors can occur through active site restoration, or in some cases, via ecological succession as landscape drivers like agriculture or other threats change in intensity across the landscape. Common threats to freshwater fishes include the degradation of in-stream habitat quality, barriers to migration due to dams or other physical obstructions, flow alteration, invasive species and the introduction of disease, climate change, and overharvesting, among many others (Dudgeon et al. 2006; Cooke et al. 2012; Grill et al. 2015; Reid et al. 2018). Ideally, the knowledge base describing the causative mechanism for a species extirpation should go beyond vague terms like ‘habitat degradation’. For example, a causative mechanism might imply that the species was extirpated due to increased siltation following the removal of riparian

vegetation, which led to restricted food supply and poor hatching success of juveniles. This finding would imply that sediment transport controls and in-stream sediment removal should be targeted as one aspect of a multi-tiered stream restoration program prior to undertaking repatriation. Below we highlight important habitat characteristics, species characteristics, fish community characteristics, stocking considerations, and monitoring considerations for imperilled fish species repatriation and identify knowledge gaps that may be leading to the underrepresentation of fish species among repatriation efforts.

Habitat characteristics

Successful repatriation efforts require a thorough understanding of species-specific habitat requirements to ensure suitable habitat exists (Bond and Lake 2003; Schumann et al. 2017). Fish habitat requirements vary depending on life stage, season, and presence of other species occupying the habitat, among others (Rosenfeld and Hatfield 2006). If suitable habitat is unavailable for any life stage, repatriation is likely wasted effort other than to confirm *a priori* expectations about habitat quality, and other conservation options need to be reconsidered (i.e., primary emphasis on habitat restoration). For many imperilled freshwater fishes, there are limited data on habitat requirements among life-stages. This stems from the challenges of detecting species that are rare or infrequent and the difficulty of conducting causative habitat studies for species at low population abundance. Repeated surveys with multiple gears and other novel sampling approaches can aid in estimating occupancy among habitat types while incorporating the problem of imperfect detection (MacKenzie et al. 2002; Royle 2004). For example, the proportion of sand and fine gravel among Canadian tributaries of Lake Erie has been shown to be an important predictor of the occupancy for the Eastern Sand Darter

(*Ammocrypta pellucida*; Dextrase et al. 2014), a *Threatened* SARA-listed species (Government of Canada 2002; Fisheries and Oceans Canada 2012). However, due to changes in the availability of sand and fine gravel habitats as a result of natural (fluvial) and anthropogenic (erosion) drivers, Eastern Sand Darter habitat can change in space and time (Ginson et al. 2015); as such, improving our understanding of how erosion, transport, and deposition influence substrate stability could greatly improve fish species repatriation efforts (Franzin et al. 2002; Ward et al. 2002).

In many cases, restoration efforts to improve imperilled freshwater fish habitat can be extremely challenging and costly (e.g., dam removal to regain historical flow regime). As well, uncertainty regarding the future habitat condition of potential repatriation sites is an important consideration for repatriation. Several studies in the northern hemisphere have demonstrated that due to the effects of warming, some freshwater fishes are shifting their distributions northwards, while other species show signs of range contraction (Comte et al. 2013; Alofs et al. 2014). Anticipating the possibility of changes in future habitat condition (e.g., temperature, turbidity) can increase the probability of long-term species conservation and recovery. Therefore, one important issue that the scientific community needs to consider is at what spatial scale are species repatriation efforts likely to succeed? Considerable scientific and ethical debate exists about introducing imperilled species outside of their native range due to the potential for unintended consequences (George et al. 2009; Ricciardi and Simberloff 2009; Lawler and Olden 2011). However, for species with extremely small natural ranges, for example several small lakes, consideration of species introductions outside the historically known distribution may be warranted to ensure future species persistence.

The recovery efforts for Atlantic Whitefish provide a unique Canadian example where repatriation efforts have occurred outside of historically occupied sites. Atlantic Whitefish is an endangered, cool-water species endemic to Nova Scotia, Canada, restricted to three interconnected lakes in the Upper Petite Rivière (Fisheries and Oceans Canada 2018). Few Atlantic Whitefish remain in the wild, with an estimated 18-38 individuals comprising the effective population size (Cook 2012; Fisheries and Oceans Canada 2018). After considerable success in captive breeding of Atlantic Whitefish, more than 12,000 individuals were released between 2005 and 2012 into a lake outside the historical range of Atlantic Whitefish. This lake, which is approximately 100 km northeast of the extant wild population, was chosen as a site for introductions because it had similar habitat characteristics to the Petite Rivière, it held available prey for the species, was devoid of threats posed by non-native Smallmouth Bass and Chain Pickerel (*Esox niger*) and was nearby the Bedford Institute of Oceanography, which offered operational benefits for the repatriation project (Bradford et al. 2015). However, despite important repatriation momentum, further research is needed to identify the degree of success for those introductions.

Species characteristics

Given the objective of establishing self-sustaining, breeding populations of imperilled species, knowledge of species life-history traits improves the likelihood of successful repatriation. For example, understanding species-specific survival rates when introducing individuals into the wild are needed to ensure stocking densities are optimized. Particularly important life-history information for imperilled fishes include age and size at maturity, duration and periodicity of spawning, degree of parental care, stage-specific growth rates, the average

number of offspring per breeding season, and species longevity, among others (Winemiller and Rose 1992). This type of information helps to inform when and how often repatriation should occur, as well as to provide population reference points during pre- and post-monitoring. For example, repatriation efforts for later maturing, larger bodied, highly fecund species with large geographic home ranges (i.e., periodic life-history strategy; Winemiller and Rose 1992) require stocking of thousands of progenies over many years. In Canada, for example, White Sturgeon has been introduced to freshwaters in southern British Columbia for several decades; approximately 284,000 individuals have been released since 1990 in the Kootenay River (Fisheries and Oceans Canada 2014b; Hildebrand et al. 2016). Alternatively, repatriation of smaller-bodied, rapidly maturing species with a shorter life span and a narrow geographic range (i.e., opportunistic life-history strategy; Winemiller and Rose 1992) requires fewer introductions (George et al. 2009). As well, information on species life-history traits provides information on the habitat types required to support life stages. For example, flow regime may be an important consideration for riverine fishes that depend on larval drift (Lechner et al. 2016). Through comparisons to historical or geographically distinct populations, information on species-specific life history can provide baselines for assessing the success of repatriation attempts.

Biotic interactions

Biotic interactions at repatriation sites can play a role in the success of repatriation efforts. In some cases, fishes may rely on co-occurring species for particular life-history processes (i.e., positive obligate or facultative biotic interactions). For example, many North American minnows are nest associates (Johnston 1994; Frimpong 2018), or spawn in nests created by other species and abandon their brood to be cared for by the nesting species. For

imperilled nest associates, failure to identify habitat that contains the required nesting substrate and conditions (e.g., flow, temperature) where species can co-occur will likely result in unsuccessful repatriation attempts. This is true for Redside Dace (*Clinostomus elongatus*) in Canada, which lays non-adhesive eggs in the gravel nests of Common Shiner (*Luxilus cornutus*) and Creek Chub (*Semotilus atromaculatus*) (COSEWIC 2007). If repatriation was to occur for Redside Dace, ensuring that potential sites for repatriation contain abundant populations of these important co-occurring species would be an important consideration.

Alternatively, both native and invasive species can represent significant barriers to the re-establishment of imperilled species through direct effects of predation or indirectly via competition for food or habitat (i.e., negative obligate, facultative, competitive, or predatory biotic interactions). For example, the establishment and abundance of Round Goby (*Neogobius melanostomus*) in the Great Lakes tributaries has been linked to declines of imperilled species, such as the Eastern Sand Darter (Raab et al. 2018). For hatchery raised game fishes released into the wild, predation has been described as one of the most important factors for failed introductions (e.g., Marsh and Brooks 1989; Buckmeier et al. 2005). As well, the risk of disease transfer from hatchery fish populations to wild populations is increased when the recipient fish community contains invasive species (Pejchar and Mooney 2009), further emphasizing the importance of understanding the local community dynamics where repatriation is to occur. Overall, repatriation efforts should aim to maximize positive biotic interactions for imperilled species while minimizing the negative interactions when selecting areas for introduction (i.e., introductions should only occur in areas where occupancy probabilities of competitor or predatory species are low).

278 *Stocking approaches*

279 Establishing populations of imperilled species requires that individual propagules are
280 introduced to the system, whether reared in a hatchery or transferred from nearby locations (i.e.,
281 translocation). Fish husbandry in a laboratory setting is challenging, particularly for imperilled
282 species (Brown and Day 2002), and only rarely has been done for species in Canada (e.g.,
283 Atlantic Whitefish, Copper Redhorse). Often, animals bred in captivity display behavioural
284 deficiencies, such as those related to foraging behaviour and predation (Snyder et al. 1996);
285 hatchery experiments have demonstrated the importance of enriching habitat complexity to
286 promote natural foraging behaviors (e.g., Rodewald et al. 2011). As well, maintaining adequate
287 levels of genetic diversity is a common problem when trying to breed hundreds to thousands of
288 individuals for introduction from a small founding population (Brown and Day 2002; George et
289 al. 2009). Although significant improvements in captive breeding of some imperilled species
290 over the last few decades have been made (Rakes et al. 1999; Shute et al. 2005; Ruble et al.
291 2014; Ruble et al. 2016), fish raised in captivity are at risk of becoming completely adapted to
292 hatchery conditions and becoming domesticated (i.e., mitigated extinction; Baumsteiger and
293 Moyle 2017).

294 Translocation of individuals from nearby populations to areas where the species was
295 extirpated represents a promising option for re-establishing fish populations (George et al. 2009).
296 However, selecting the right source population(s) for translocation efforts can dictate whether
297 repatriation efforts are successful (Minckley 1995). Simply choosing a population by geographic
298 distance alone neglects aspects of local adaptation. Instead, evaluating the degree of genetic
299 diversity and potential for adaptation of surrounding populations is critical (He et al. 2016).
300 Local adaptation to environmental characteristics tends to be positively correlated between

geographically distinct populations (Houde et al. 2015), and therefore, efforts to identify suitable founding populations for translocation should start in areas with similar habitat. When suitable populations from similar habitat are unavailable, choosing the right source population becomes a bet-hedging strategy, searching for sources with the greatest heritable variation or adaptive potential while considering the impacts of removing individuals (Allendorf 1991).

Additionally, the size and density of fish at the time of release and the number of stocking events over time are commonly identified factors related to the success of stocking recreational species (Cowx 1994) and introducing or re-establishing fish populations (Cochran-Biederman et al. 2015). Larger, older fish tend to show the greatest survival after being introduced into the wild and successful repatriation efforts have typically introduced species on a yearly basis (George et al. 2009). There is a long history of experimenting with stocking strategies for recreational species to achieve desired population attributes (Swingle 1951; Modde 1980; Cowx 1994), though this information is virtually absent for non-recreational or non-commercial species. However, as is most often the case, decisions related to the number and age of fish to release, and frequency of such introductions, are often limited by resources (e.g., space and cost limitations of rearing individuals). Further research is needed to better understand the optimal density of fish for successful introductions of imperilled species, as well as trade-offs of removal from source populations if undertaking simple translocations (e.g., Todd and Lintermans 2015). Many key questions remain, such as whether repatriation efforts should attempt to introduce fish from differing age-classes in proportion to the age-class structure of surrounding populations? Questions related to stocking dynamics can be aided with the use of models, such as population viability analyses, to explore the implications of one-time vs. multiple stocking events across different propagule densities and age classes.

Monitoring

Monitoring is essential for evaluating the success or failure of any management measure, including repatriation. Prior to initiating repatriation and monitoring efforts, it is important to identify what metrics will be used to assess success or failure (Armstrong and Seddon 2008). These might include simple detection of the species in the years following release, estimates of survival over time (i.e., mark-recapture), observations of spawning activity, or identification of recruitment into the breeding population (Cochran-Biederman et al. 2015). In addition to monitoring the repatriated biota, it is also important to monitor the habitat characteristics that originally supported the introduction of that species. It should be acknowledged from the start that repatriation monitoring is a long-term affair. One of the earliest successful efforts of imperilled species propagation and repatriation in North America took place for Abrams Creek in the United States Great Smoky Mountains National Park (Shute et al. 2005; George et al. 2009). Over 20-years, thousands of Smoky Madtom (*Noturus baileyi*), Yellowfin Madtom (*N. flavipinnis*), Citico Darter (*Etheostoma sitikuense*), and Spotfin Chub (*Erimonax monachus*) were released. However, it took almost five years before any of the released fishes were recaptured and 10 years before in-stream recruitment was recorded (George et al. 2009). Several studies have recommended that at least 10 years of monitoring is needed for measuring repatriation success (Godefroid et al. 2011; Houde et al. 2016), though this timeframe will vary based on the generation time of the species in question.

Hierarchical challenges when approaching repatriation initiatives.

There are several approaches to repatriation that are presumed to vary hierarchically in their complexity, likelihood of success, and financial cost (Figure 2). At the basis of repatriation efforts are habitat restoration efforts to support the various life-history stages of the imperilled species. Although not a repatriation strategy per se, habitat restoration can lead to species recovery by natural dispersal from locally-connected populations (Letcher et al. 2007). The degree to which habitat restoration alone can lead to the reestablishment of imperilled populations will depend on many different factors including the degree of species and habitat impairment at and nearby the restoration site, as well as the level of connectivity among habitats, among others. Enhancing connectivity has become increasingly recognized as an important conservation strategy as climate change continues to alter local habitat conditions (Doerr et al. 2011). In some cases, connectivity may facilitate dispersal of native species, but if not considered carefully, can also facilitate movement of invasive species or native predators or competitors (e.g., control of Sea Lamprey (*Petromyzon marinus*) movement; Milt et al. 2018). Alternatively, there is also growing evidence that construction of barriers can facilitate invasion success by altering environmental conditions and creating opportunities for invaders by opening novel niche space (Liew et al. 2016; Raab et al. 2018).

Habitat restoration may be insufficient to recover species at historically occupied locations if natural colonization is unlikely. However, habitat restoration is a prerequisite for successful repatriation efforts. Once habitat restoration has occurred and habitat quality is deemed suitable for the species in question, the simplest approach is translocation of individuals from geographically proximate populations. In addition to uncertainty about the effect of habitat restoration, the success of translocation efforts from geographically proximate populations can vary due to the availability of suitable rescue populations that may have different local

adaptations from the historical population. Along with ensuring that the translocated population can adapt to conditions at repatriation sites, it is equally important to understand the effects of removals on the donor population (Todd and Lintermans 2015; Lusardi and Moyle 2017). Increasing in complexity, translocations from geographically distant populations are less likely to be successful than translocating geographically proximate populations and can impose the potential for unintended effects (e.g., inbreeding depression). The act of transportation and acquiring the permits to cross regional borders makes translocations from geographically disparate populations more expensive and logistically challenging (George et al. 2009) than nearby populations. Furthermore, geographically disparate populations may have local adaptations that could reduce the likelihood of establishing a breeding population.

If translocations are not feasible, captive breeding programs may be required. Initiating a captive breeding program is expensive, increases the likelihood of unintended genetic consequences, and there are substantial challenges that limit the relative likelihood of success (Snyder et al. 1996; Brown and Day 2002). For imperilled species, ensuring that captive populations maintain adequate genetic diversity and natural behavioural tendencies for future release can be challenging. Establishing a sufficiently large founding population can aid in maintaining captive stock diversity, and hence may also increase the likelihood of success, but requires larger breeding facilities. While there are challenges to captive breeding and rearing, captive breeding programs do provide a key benefit – a large source of propagules for release. However, the steps required to initiate and maintain a captive breeding program can be costly (Snyder et al. 1996), and therefore, restrict the scope of this strategy for the most dire conservation scenarios. Overall, as the status of imperilled species decreases, the costs of repatriation increases, and the potential success of those efforts becomes less likely.

The future of freshwater fish repatriation in Canada

Freshwater fishes are of high conservation concern (Baillie et al. 2010; Burkhead 2012) and as a result, on-the-ground conservation efforts require a diversity of strategies – repatriation represents one of these strategies. The initial priority for recovering an imperilled fish species should be understanding the causative mechanisms associated with population loss, followed by targeted strategies to address the issue, such as habitat restoration (Figure 2). Without the necessary abiotic and biotic features, imperilled fish repatriation efforts are bound for failure, further contributing to the ongoing cycle of population loss while minimizing the opportunity for learning.

There remain many unanswered questions about why certain repatriation attempts are more successful than others. Many of the critical questions proposed by Armstrong and Seddon (2008) are still relevant today, yet remain unanswered (Taylor et al. 2017; Figure 3). For example, how many individuals should be harvested from a source population and what is the best way to allocate those individuals across repatriation sites (Armstrong and Seddon 2008)? Although a great deal of work has been dedicated to species repatriation, most efforts have not been undertaken in an experimental framework, limiting the degree of learning and hypothesis testing. Taking an adaptive management approach through experimental studies could be used to increase our knowledge and understanding of the factors limiting or promoting success, to confirm *a priori* expectations, and to understand elements of habitat quality and stocking density that may be difficult to tease out in the absence of such experiments (e.g., Atlantic Whitefish in Nova Scotia). However, an adaptive approach for imperilled species requires the collective

understanding among scientists and policy-makers alike that some efforts will fail, but in doing so, provide the opportunity to maximize learning and improve future conservation decisions.

Across the suite of taxa identified for repatriation efforts, freshwater fishes provide an ideal study system for informing open questions in repatriation science. There are several advantages for using fish as a model system (Power 1989): (1) fishes, particularly those that are imperilled, are often relatively small (Angermeier 1995; Olden et al. 2007) and therefore can be maintained in reasonably-sized lab and transport facilities; (2) the number of individuals available for establishing native fish communities can be more easily controlled and manipulated to provide experimental replicates; and, (3) habitat characteristics (e.g., temperature, water clarity, substrate) can be manipulated in the laboratory setting to test for differences in reproductive success and survival across habitat types. This has long been the strategy for stocking recreationally- and commercially-important species. As well, given the feasibility of manipulating abiotic and biotic factors using closed experimental ponds or streams (e.g., Bestgen et al. 2010), freshwater fish repatriation studies could provide the needed model for facilitating cross-system comparisons and answering important open questions in conservation biology (Armstrong and Seddon 2008; Figure 3), such as the relative roles of habitat quality and inoculation density. Experimental trials can occur in the wild by intentionally releasing imperilled species to different habitats in formerly occupied areas across a gradient of suitability to confirm *a priori* expectations and perhaps learn about species-specific environmental thresholds.

Despite considerable information needs related to the ecological themes presented above, we have been tremendously successful at supplementing and establishing recreationally important fish populations around the globe. There are several examples where repatriation has

succeeded for imperilled fishes in North America. Efforts to repatriate freshwater fishes have been successful for Smoky Madtom, Yellowfin Madtom, and Citico Darter in the Great Smoky Mountains National Park, Watercress Darter (*Etheostoma nuchale*) in Alabama, Mirror Shiner (*Notropis spectrunculus*), Saffron Shiner (*N. rubricroceus*), Silver Shiner (*N. photogenis*), Telescope Shiner (*N. telescopus*), Tennessee Shiner (*N. leuciodus*), and Gilt Darter (*Percina evides*) in North Carolina, and Lake Sturgeon (*Acipenser fulvescens*) in the Mississippi River, among others (George et al. 2009; Buszkiewicz et al. 2016). However, examples of successful repatriation attempts are rare in Canada, especially among SARA-listed freshwater fishes. In Canada, repatriation and/or population supplementation efforts for SARA-listed freshwater fishes have been initiated for Atlantic Whitefish, Copper Redhorse, Striped Bass, Westslope Cutthroat Trout, and White Sturgeon, though further investigations are needed to identify the success of such efforts.

To conclude, fishes have been introduced to freshwater ecosystems for centuries. Given the global trend of freshwater fish declines and promising case studies of repatriation success, now is the time to focus research interest on re-establishing native stocks. Repatriation represents an important tool in the species recovery toolbox, but its application requires a thorough understanding of the local abiotic and biotic conditions that promote the persistence of the species in question. For some imperilled species, the time needed to fill these information gaps and further delay potential repatriation efforts could ultimately lead to local extirpations, or worse, extinctions. For such species, adaptive approaches, similar to those taken for recreationally and commercially important species, are needed to promote species recovery.

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698 **Figure Captions**

699 **Figure 1.** Total number of repatriation, supplementation, or translocation efforts initiated,
700 identified as a potential recovery strategy, or not identified as a potential recovery strategy for
701 Species at Risk in Canada.

702 **Figure 2.** Conceptual relationships between the relative likelihood of success and relative
703 ecological complexity among repatriation efforts. Ecological complexity is used as a proxy to
704 generalize the hierarchical challenges associated with repatriation such as the increased potential
705 for unintended negative effects (e.g., extirpation of source populations, introduction of disease)
706 and the challenges associated with on-the-ground management efforts (e.g., financial costs).
707 With increased complexity comes increased uncertainty.

708 **Figure 3.** Ten key questions for the repatriation of fishes in Canada, divided into questions about
709 habitat characteristics, species characteristics, biotic interactions, stocking approaches, and
710 monitoring.

711 **Figure 1.**

712

713 **Figure 2.**

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715 **Figure 3.**

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