Int. J. Lim. 2024, 60, 5
© D.B. Bunnel *et al.*, published by EDP Sciences, 2024
https://doi.org/10.1051/limn/2024002

Available online at:
www.limnology-journal.org

Special issue - Biology and Management of Coregonid Fishes
Guest editors: Orlane Anneville, Chloé Goulon, Juha Karjalainen, Jean Guillard, Jared T. Myers and Jason Stockwell

RESEARCH ARTICLE OPEN ACCESS

How diverse is the toolbox? A review of management actions to conserve or restore coregonines

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Received: 27 November 2023; Accepted: 7 February 2024

Abstract – Over the past centuries, coregonines have been exposed to a range of stressors that have led to extinctions, extirpations, and speciation reversals. Given that some populations remain at risk and fishery managers have begun restoring coregonines where they have been extirpated, we reviewed the primary and gray literature to describe the diversity of coregonine restoration or conservation actions that have been previously used. Although stocking of hatchery-reared fish has been commonly used for supplementing existing coregonine fisheries, we considered stocking efforts only with specifically conservation or restoration goals. Likewise, conservation-driven efforts of translocation were not widespread, except in the United Kingdom for the creation of refuge populations to supplement the distribution of declining stocks. Habitat restoration efforts have occurred more broadly and have included improving spawning habitat, connectivity, or nutrient concentrations. Although harvest regulations are commonly used to regulate coregonine fisheries, we found fewer examples of the creation of protected areas or outright closures. Finally, interactions with invasive species can be a considerable stressor, yet we found relatively few examples of invasive species control undertaken for the direct benefit of coregonines. In conclusion, our review of the literature and prior Coregonid symposia revealed relatively limited direct emphasis on coregonine conservation or restoration relative to more traditional fishery approaches (*e.g.*, supplementation of fisheries, stock assessment) or studying life history and genetics. Ideally, by providing this broad review of conservation and restoration strategies, future management efforts will benefit from learning about a greater diversity of potential actions that could be locally applied.

Keywords: whitefish / cisco / stocking / habitat restoration / biodiversity

1 Introduction

Freshwater fish and fisheries occupying both lotic and lentic habitats have endured a litany of human-induced stressors over the past century (see Reid *et al.*, 2018; Díaz *et al.*, 2019; Birk *et al.*, 2020). As a result, the rate of extinctions in freshwater fish species is higher than in most other habitats (Strayer and Dudgeon, 2010; Burkhead, 2012; Darwall and Freyhof, 2016). Species in the sub-family Coregoninae (hereafter, coregonines) are widely distributed in circumpolar, northern lentic and lotic habitats (*i.e.*, region of North America, Europe and Asia) and are emblematic of fish and fisheries challenged by anthropogenic stressors. Species

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Table 1. Description of queries used to identify peer-reviewed literature and reports describing coregonine conservation or restoration efforts.

Search engine	1st word	2nd word	3rd word
Google scholar	whitefish	restoration	
	whitefish	conservation	
	whitefish	habitat	restoration
	whitefish	refuge	
	whitefish	harvest	regulation
	cisco	restoration	
	cisco	conservation	
	cisco	refuge	
	cisco	habitat	restoration
	cisco	harvest	regulation
Web of science	coregon*	restor*	stock*
	coregon*	conserv*	stock*
	coregon*	restor*	habitat*
	coregon*	conserv*	habitat*
	coregon*	restor*	invas*
	coregon*	conserv*	invas*
	coregon*	restor*	harvest
	coregon*	conserv*	harvest
	cisco	restor*	stock*
	cisco	conserv*	stock*
	cisco	restor*	habitat*
	cisco	conserv*	habitat*
	cisco	restor*	invas*
	cisco	conserv*	invas*
	cisco	restor*	harvest
	cisco	conserv*	harvest
	whitefish	restor*	stock*
	whitefish	conserv*	stock*
	whitefish	restor*	habitat*
	whitefish	conserv*	habitat*
	whitefish	restor*	invas*
	whitefish	conserv*	invas*
	whitefish	restor*	harvest
	whitefish	conserv*	harvest

and population extinctions of coregonines are common in both North America (Bailey and Smith, 1981; Eshenroder *et al.*, 2016; Bunnell *et al.*, 2023) and Europe (Steinmann, 1950; Freyhof and Schöter, 2005; Vonlanthen *et al.*, 2012) owing to exposure to various stressors. One of the primary stressors has been eutrophication, which can have multiple negative effects on populations. First, eutrophication can lead to insufficient oxygen concentrations in preferred deeper waters, causing coregonines to occupy potentially lethal warmer shallower water and lead to population declines or extirpations (*e.g.*, Evans *et al.*, 1996; Kumar *et al.*, 2013; Lyons *et al.*, 2018). Furthermore, eutrophication can reduce egg survival within the diffusive boundary layer when carbon-rich sediments cause high oxygen uptake (Ventling-Schwank and Müller, 1991; Müller, 1992; Müller and Stadelmann, 2004; Wahl and Löffler, 2009). In lakes harboring multiple species, eutrophication can also result in speciation reversal if natural selection forces leading to ecological speciation are relaxed (Vonlanthen *et al.*, 2012; Frei *et al.*, 2022). Beyond nutrient pollution, other anthropogenic stressors, including sedimentation or the construction of dams, have led to the deterioration or even blockage of spawning and nursery habitats (Steinmann, 1950; Ventling-Schwank and Livingstone, 1994; Winfield, 2004; Haakana and Huuskonen, 2012; Schaefer *et al.*, 2022). Negative interactions with invasive species also have contributed to declines in coregonines, affecting multiple life stages from eggs to adults (*e.g.*, Christie, 1973; Hrabik *et al.*, 1998; Myers *et al.*, 2009; Bhat *et al.*, 2014; Rösch *et al.*, 2018; Cunningham and Dunlop, 2023). Overfishing also was likely a primary driver of the loss of some coregonines in both North America (Smith, 1964; Eshenroder *et al.*, 2016) and Europe (Dottrens, 1950; Steinmann, 1950; Bardel, 1956; Laurent, 1972) in the 20th century. Another challenge to maintaining biodiversity has been introgression arising from erroneous or intentional stocking of more common European whitefish species into areas with more rare, locally adapted whitefish species (*e.g.*, Douglas and Brunner, 2002; Hudson *et al.*, 2011; Dierking *et al.*, 2014; Selz and Seehausen, 2023). Finally, climate change (*e.g.*, declining ice cover, increased occurrence of high rainfall events or droughts, warming water temperature, shorter lake turnover time) poses a relatively new and emerging threat to coregonine sustainability for fishery managers to consider (Elliott and Bell, 2011; Jacobson *et al.*, 2012; Salmaso *et al.*, 2018; Brown *et al.*, 2022).

Within the broad distribution of coregonines, some historically important stressors have been improving in recent decades. For example, many ecosystems that once experienced eutrophication are now undergoing oligotrophication owing to stricter regulations on nutrient inputs (Anderson *et al.*, 2005; Bunnell *et al.*, 2014). These regulations have led to widespread ecosystem benefits (*e.g.*, better water quality, increased recreational opportunities), including improved oxythermal habitat for many coregonine species (*e.g.*, Gerdeaux *et al.*, 2006; Madenjian *et al.*, 2011) that, in some cases, has led to the re-emergence of coregonine diversity (*e.g.*, Müller, 2007; Jacobs *et al.*, 2019). Another emerging trend in some countries is the removal of dams, many of which are deteriorating and considered too expensive to maintain (O'Connor *et al.*, 2015). Coregonines are one of several groups of fishes that can benefit from the removal of dams or construction of fish passages by colonizing new upstream habitat (*e.g.*, Kiffney *et al.*, 2018). In other ecosystems, fishery managers have sought to improve the spawning substrate of lithophilic spawners (primarily salmonids), by either enhancing habitat or even building new reefs (*e.g.*, Tolentino and Moon, 2012; Fischer *et al.*, 2018; Baetz *et al.*, 2020). An increasing awareness of the potential for habitat enhancement to facilitate fish production, even over more traditional tools such as stocking, was supported by a recent replicated, 6 yr, 20-lake experiment in Germany (Radinger *et al.*, 2023).

Over the last several decades, many countries have passed conservation legislation to protect the environment, as well as imperiled fish populations (including coregonines) and their habitat. For example, in the United Kingdom (U.K.) managers have sought to preserve the limited number of *Coregonus lavaretus* (Linnaeus; Common whitefish or European whitefish) and *C. albula* (Linnaeus; Vendace or European cisco) populations that remain on the islands (Winfield *et al.*, 2002; Winfield *et al.*, 2012; Winfield *et al.*, 2013a). In Nova Scotia, Canada, managers are seeking to conserve endangered *C. huntsmani* (Scott; Atlantic whitefish) that are restricted to three lakes within one watershed now that connectivity has become reduced (Fisheries and Oceans Canada, 2018). Restoration, on the other hand, can be broadly defined as actions to help an ecosystem that has been damaged, degraded, or destroyed (see Society for Ecological Restoration: https://ser-rrc.org/what-is-ecological-restoration/), which could include reintroducing extirpated species. An example of restoration is in the Laurentian Great Lakes, where fishery managers recently endorsed an adaptive management strategy to restore *Coregonus* spp. (see Bunnell *et al.*, 2023) and where *C. hoyi* (Milner; Bloater) in Lake Ontario (Canada, United States (U.S.): 43.638, −77.811) are currently being reintroduced from existing populations in Lake Michigan (U.S.: 43.900, −87.044; Weidel *et al.*, 2022).

Given the recent momentum towards coregonine conservation and restoration, we sought to conduct a review of the management actions that have been undertaken to conserve imperiled coregonine populations or restore coregonines that have been locally extirpated. For the purposes of this review, we generally will not distinguish between restoration or conservation because our goal is to summarize any tools and actions that have been used to potentially support either management action. We argue that a comprehensive survey and review could be helpful for emerging coregonine restoration efforts in the Laurentian Great Lakes and future conservation or restoration efforts across their broader distribution. We emphasize that coregonine fishery management actions where the primary short-term objective was the supplementation or creation of fisheries was beyond the scope of this paper. For example, studies describing stocking of hatchery-reared fish to support fisheries (even when conservation genetics are evaluated therein) would not be included in this paper. We note, however, that several studies have evaluated the efficacy of stocking on coregonine yield or year-class strength: some reporting little or no effect (Christie, 1963; Salojärvi, 1992; Wanke *et al.*, 2017, Baer *et al.*, 2023), whereas others reporting increased harvest (Anneville *et al.*, 2009; Wanke *et al.*, 2016; Wedekind *et al.*, 2022).

Herein, our approach was to first use online databases of scholarly literature (Google Scholar, Web of Science) to identify peer-reviewed papers and reports using key words inclusive of coregonine taxonomy and conservation and restoration tools (see Tab. 1). Next, we searched the titles of the 14 previous Coregonid Symposia proceedings (*i.e.*, Biology and Management of Coregonid fishes) that have been published starting from 1970 (*e.g.*, Lindsey and Woods, 1970) through 2021 (Karjalainen *et al.*, 2021). Since the 1995 proceedings (*e.g.*, Luczynski *et al.*, 1995), the titles have been organized in a table of contents by theme area; we recorded the names or key phrases used in all theme areas to create a "wordcloud" to depict the most common words or phrases that have been used. Finally, we supplemented our review by recruiting co-authors with regional expertise to help us uncover unpublished, "gray" literature. Attempts to access more regional experts from Asia were unsuccessful.

This review is organized below by different categories of fishery management actions for the purposes of conservation or restoration: 1) stocking of hatchery-reared fish; 2) translocation of wild fish (at multiple life stages) to new ecosystems; 3) habitat restoration, including improving spawning areas, connectivity, or nutrients concentrations; 4) eliminating harvest or the creation of protected areas; and 5) the control of invasive species. We conclude this review by assessing how frequently each action has been used and by providing some suggestions for future consideration. Ideally, by providing this broad review, future coregonine restoration or conservation efforts can be better informed about the diversity of options that could be locally applied within their jurisdictions.

2 Stocking of hatchery-reared fish

Stocking of hatchery-reared coregonines is widespread throughout its range and dates to the 19th century (*e.g.*, Ilmast and Sterligova, 2004; Eckmann, 2012; Wood, 2016). Although we use the term "hatchery-reared" for simplicity, we acknowledge that the time spent in hatcheries can be quite variable across coregonine rearing practices. For example, many agencies rear fish in hatcheries from embryos to late-stage juveniles prior to stocking, whereas other agencies move hatchery-reared larvae into rearing ponds where they can experience more natural food supplies and photoperiod conditions before being stocked (*e.g.*, Gerdeaux, 2004; Leskelä *et al.*, 2004). Regardless of rearing method, the primary goal of most hatchery-reared coregonines to be stocked has been for the creation or supplementation of fisheries rather than conservation or restoration (*e.g.*, Müller and Stadelmann, 2004; Wood, 2016; Wedekind *et al.*, 2022). Perhaps not surprising given its prevalence, coregonine stocking can lead to negative impacts on other native fishes (Svärdson, 1976; Sandlund *et al.*, 2013) but also on existing coregonine populations through its potential to reduce genetic diversity through introgression or hybridization, selection towards undesirable traits, or introduction of disease (see Waples, 1991; Kahilainen *et al.*, 2011; McMillan *et al.*, 2023). As a result, we found that the most common use of stocking hatchery-reared fish in the realm of conservation or restoration was for reintroducing extirpated populations. Furthermore, ideally a reintroduction would not occur unless all previous threats that led to their extirpation have been removed and a population viability analysis has occurred (see Bunnell *et al.*, 2023).

In Europe, one restoration example is the re-introduction of anadromous *C. oxyrinchus* (Linnaeus; North Sea Houting) into the German section of the Rhine River (54.926, 8.714), where it was extirpated owing to overfishing and habitat degradation (*e.g.*, eutrophication, dams) in the 1940s (De Groot and Nijssen, 1997). Because many of these stressors had been ameliorated by the 1980s, *C. oxyrinchus* from one population that has persisted in the river Vidå (Denmark: 54.926, 8.714) was reared in hatcheries and stocked into the Rhine beginning in the late 1990s and early 2000s and evidence for natural reproduction has been provided (Borcherding *et al.*, 2010). Although our use of this example is to illustrate the use of stocking for the intent of reintroduction, we should acknowledge ongoing scientific debate regarding *C. oxyrinchus*. First, one study has argued that the population from the Vidå is *C. maraena* (Bloch; Maraena whitefish), instead of *C. oxyrinchus*, based on morphological data (Freyhof and Schöter, 2005) although Hertz *et al.* (2019) noted the need for additional genetic evidence. Second, Kroes *et al.* (2023) recently used mitochondrial DNA evidence from historical and contemporary samples to argue that *C. oxyrinchus* should not be considered its own species (and therefore 'extinct') because they found minimal genetic differentiation from *C. lavaretus*.

In North America, one example of using hatchery-reared fish for reintroduction was for *Prosopium cylindraceum* (Pennant; Round Whitefish) in water bodies throughout the Adirondack region (~ 44.125, −73.869) of the U.S. They once were distributed in more than 80 lakes or ponds in this region, but became extirpated in 75 of them by the early 2000s owing primarily to negative interactions with invasive species or acidification of the lakes (Steinhart *et al.*, 2007). The state of New York instituted a reintroduction program using hatchery-reared fish that targeted 24 of these 75 lakes, but has documented natural reproduction in only four of them to date (Conley *et al.*, 2021; Holst, 2023). Another example is in Lake Ontario where a multi-agency team initiated the reintroduction of *C. hoyi* in 2012 through stocking of hatchery-reared animals originating from Lake Michigan (see Weidel *et al.*, 2022). The first decade of the program has focused on developing hatchery-rearing, stocking, and monitoring programs that would allow the management agencies to implement a lake-wide restoration program. The initial objectives of the program have been met and there is positive momentum in many areas (*e.g.*, rearing success, evidence of some survival based on limited recaptures of stocked fish), however, there are still some challenges to overcome (*e.g.*, potentially poor survival of stocked fish and difficulty maintaining captive broodstock, Weidel *et al.*, 2022). Lake Ontario fishery managers are developing a more detailed restoration strategy based on past successes and lessons learned since 2012 (C. Legard, New York State Department of Environmental Conservation, personal communication, November 9, 2023), consistent with the adaptive nature of the Laurentian Great Lakes Coregonine restoration framework (Bunnell *et al.*, 2023).

Another example from North America is an ongoing effort in Nova Scotia, Canada, to conserve endangered anadromous *C. huntsmani* (Fisheries and Oceans Canada, 2018), which only occurs within one of its two original watersheds in Nova Scotia owing to negative interactions with invasive piscivorous species, acidification of the aquatic habitat, and barriers to inland spawning habitats (COSEWIC, 2010). One of the strategies was an attempt to create a "back-up" (also known as "refuge") population by stocking hatchery-reared fishes from 2005-2008 in Anderson Lake (44.727, −63.620), which is outside of its known range. As of 2018, no evidence of an established refuge population had been confirmed (Fisheries and Oceans Canada, 2018).

One other case study in the U.S. waters of Lake Huron (44.816, −82.849) illustrates the management concern of seeking to avoid introgression when using hatchery-reared fish for a reintroduction program. *C. artedi* (Lesueur; Cisco) once enjoyed a lake-wide distribution in this large water body in the early 20th century, but several environmental stressors caused it to become extirpated within one of its most important habitats, Saginaw Bay (43.970, −83.504), by the 1950s (Cottrill *et al.*, 2020; Kao *et al.*, 2022). In 2018, fishery managers began a "reintroduction" of *C. artedi* into Saginaw Bay to enhance its distribution within the main basin. We acknowledge that this could also be classified as a conservation action given that *C. artedi* is present in other parts of Lake Huron but has failed to colonize this historically important embayment over the past several decades. Hence, this effort has involved collecting gametes in the Les Cheneaux Islands region (45.956, −84.312) of Lake Huron (more than 265 km from Saginaw Bay), rearing those animals in the hatchery until they are juveniles (<100 mm total length), and then stocking them in Saginaw Bay. Fishery managers chose to start the program with gametes from the same lake rather than using gametes from another lake owing to concerns about outbreeding depression, given the potential that any reintroduced *C. artedi* from another lake could eventually reproduce with the locally adapted northern Lake Huron stock and reduce its genetic diversity (Lake Huron Technical Committee, 2023). Evidence of success has recently emerged with the recapture of nearly 50 mature hatchery-origin fish in Saginaw Bay during the 2022 spawning season (J. Bonilla-Gomez, personal communication, January 23, 2024).

Any additions of hatchery-reared coregonines would benefit from the use of conservation-based rearing practices that seek to lessen potential negative genetic or ecological effects (*e.g.*, Flagg and Nash, 1999). There are many examples where introgression between hatchery reared coregonines and wild coregonines has occurred (see Winkler *et al.*, 2011; Anneville *et al.*, 2015). Wedekind *et al.* (2022) offers a comprehensive review of the risks that can occur with stocking hatchery reared fishes that can be applied to coregonines. Eckmann (2012) argued that the stocking of *C. lavaretus* in Lake Constance (Germany, Switzerland: 47.616, 9.415) may be leading to hatchery fish outcompeting wild recruits and could be inducing unwanted evolutionary changes by using less than 10% of possible spawners when making hatchery crosses. Likewise, Hirsch *et al.* (2013) argued that the hatchery-reared fish do not represent the known within-species diversity of *C. lavaretus* in the lake (*e.g.*, spawners should be collected from both shallower and deeper regions). Finally, it can be logistically difficult and cost prohibitive to replicate the natural temperatures under which hatchery coregonine embryos and larvae are incubated and reared, respectively. Recent studies have demonstrated that both the water temperature during egg incubation and its variability can affect coregonine embryonic development (Lim *et al.*, 2017), larval survival (Stewart *et al.*, 2022), and even growth and muscle mass achieved at later life stages (Steinbacher *et al.*, 2017). Given these potential challenges and risks in rearing hatchery-reared animals for restoration or conservation purposes, it is not surprising the fishery managers have sought out other conservation or restoration tools or strategies to achieve their objectives.

3 Translocations

Translocating wildlife to new ecosystems for the purpose of restoration or conservation has enjoyed some high-profile successes (Morris *et al.*, 2021; Seddon, 2023). As a restoration or conservation strategy for aquatic ecosystems, the movement of fish directly between water bodies (*i.e.*, translocation) or minimizing how much time early life stages spend in the hatchery (*i.e.*, stocking unfed, yolk-sac larvae or rearing larvae in natural ponds with natural food) can be advantageous because it does not encumber the resources associated with rearing while also limiting the potential for artificial selection (*i.e.*, selection of traits for the hatchery rather than in the wild, see Flagg and Nash, 1999). At the same time, translocation may increase the risks associated with movement of unwanted pathogens or parasites between water bodies (Cunningham, 1996; Sainsbury and Vaughan-Higgins, 2012; Gaywood and Stanley-Price, 2023). Additionally, if too few fish are successfully translocated, this can lead to population bottlenecks which can result in high levels of inbreeding and loss of genetic diversity which, in turn, can negatively affect the long-term viability of translocated populations (Stockwell *et al.*, 1996; Furlan *et al.*, 2020; Præbel *et al.*, 2021). The only examples we found where translocations were directly used for coregonines in a conservation or restoration context was in the U.K. (see overviews in Maitland and Lyle, 2013; Adams *et al.*, 2014). The recommended criteria to facilitate translocation with minimal impact on the source population is described in Maitland and Lyle (1992) and the recommended criteria to select receptor sites is described in Adams *et al.* (2014).

Within the U.K., the primary objective of translocations was to increase the distribution and long-term security of endangered *C. lavaretus* and C. *albula* stocks by creating "refuge" populations. Almost all of these have involved the establishment of new populations in reservoirs where no damage can be done to native biodiversity but where conditions are likely sufficient for completion of coregonine life cycles. Maitland and Lyle (1990) described the limited native distribution of *C. lavaretus* in only seven water bodies-two in Scotland (Loch Lomond (56.074, −4.595) and Loch Eck (56.082, −4.994), where *C. lavaretus* is known locally as Powan), four in England (known locally as Schelly), and one in Wales (known locally as Gwyniad). Despite being described as three separate species (see Kottelat and Freyhof, 2007) and included as such within the International Union for Conservation of Nature Red List, Crotti *et al.* (2020, 2021a) could find no genetic evidence to support this conclusion. The first attempt to create "refuge" *C. lavaretus* populations used donor stock from Loch Lomond in Scotland, and transferred eggs, embryos, juveniles, and adults to two other water bodies within the Loch Lomond watershed (*i.e.*, Carron Valley Reservoir (56.030, −4.101) and Loch Sloy (56.273, −4.777); Maitland and Lyle, 1990, 1992). Despite translocating less than 15,000 unfed, yolk-sac larvae (with limited hatchery rearing) and/or 100 adults to these two Scottish refuge water bodies between 1988-1991, the creation of self-sustaining refuge populations was successful. Sampling between 2005-2006 revealed differences in head morphology, size, and growth among the source population and the two refuge populations (Etheridge *et al.*, 2010). Whether these morphological or ecological changes in the refuge populations were due to founder effects owing to limited genetic diversity during translocation, differential selection in the new habitat, genetic drift, or phenotypic plasticity was not clear, but Etheridge *et al.* (2010) discussed how further divergences between the Loch Lomond donor stock and refuge populations could limit the usefulness of the creation of refuge stocks.

The Scottish conservation program for *C. lavaretus* continued in 2007 when stressors increased for Loch Eck and one of the original refuge populations (Adams *et al.*, 2014). The first step was a suitability study to determine ideal refuge lakes, ideally with characteristics including 1) being sufficient size and depth to provide coolwater habitat, 2) having limited water drawdown during egg incubation, 3) being oligotrophic to mesotrophic in productivity, 4) having a fish community with no *Salvelinus alpinus* (Linnaeus; Arctic charr), *Esox lucius* (Linnaeus; Northern pike), *Perca fluviatilis* (Linnaeus; Perch), and *Gymnocephalus cernuus* (Linnaeus; Ruffe) (Adams *et al.*, 2014). Based on this study, four reservoirs received translocations of eggs, yolk-sac, unfed larvae (with limited hatchery rearing) and adults of *C. lavaretus* between 2009 and 2011; two received animals from Loch Lomond and two received animals from Loch Eck. By 2017, Crotti *et al.* (2021b) collected *C. lavaretus* from all source and refuge lakes and sought to determine whether there were differences genetically, morphologically, and ecologically (with stable isotopes). Similar to Etheridge *et al.* (2010), differences in fish shape were detected between the source and refuge populations. But Crotti *et al.* (2021b) also revealed novel differences in their ecological niches, likely owing to more diverse diets in the refuge populations. Genetic differentiation between source and refuge populations was relatively low, however genetic diversity was reduced in refuge populations relative to the source populations (Crotti *et al.*, 2021b; Præbel *et al.*, 2021). Interestingly, there was also evidence of some new genetic diversity arising in the refuge populations, owing either to drift (Præbel *et al.*, 2021) or potentially even local adaptation (Crotti *et al.*, 2021b). These findings were consistent with Adams *et al.* (2016) that revealed the genetic differences in *C. lavaretus* between its two native populations (Lochs Lemond and Eck) and relatively weak within-lake genetic structuring within the Loch Lomond population. Furthermore, small estimates of effective population sizes for lochs Lomond and Eck (Adams *et al.*, 2016) suggest limited capacity to adapt to future environmental change and, perhaps even more limited capacity for their refuge populations. The rigorous evaluations of these translocation efforts revealed the importance of avoiding founder effects by seeking to translocate relatively large numbers (*e.g.*, >100) of genetically representative animals (Fischer and Lindenmayer, 2000) to not only maximize survival but also to prevent bottlenecks and founder effects in the refuge populations.

Another *C. lavaretus* translocation effort was undertaken in Wales, where a native population only existed in Llyn Tegid (52.888, −3.623). Thomas *et al.* (2013) described how the population had remained relatively stable despite several stressors, including periodic hypoxic conditions, potentially detrimental water level fluctuations, and the introduction of *G. cernuus* (an egg predator). Following the precautionary approach, however, managers sought to create a refuge population by translocating more than 80,000 embryos (crossed from 366 males and 50 females) to nearby Llyn Arenig Fawr (52.927, −3.717) between 2005-2007. Evaluations revealed high egg hatching rates and the presence of one gravid female during a 2009 sampling survey (Thomas *et al.*, 2013). Subsequent sampling in 2012 revealed two additional age-1 fish sampled providing further evidence that the translocation not only produced adult fish but that those fishes were ultimately successful in their own reproduction by at least 2011 (Winfield *et al.*, 2013c).

A final translocation effort for *C. lavaretus* was undertaken in England where the Haweswater reservoir (54.521, −2.803) population was of conservation concern. The goal was to create two refuge populations in two lakes in the same watershed that were believed to be environmentally suitable. The details are described in Winfield *et al.* (1997), but are summarized below. Spawning *C. lavaretus* were caught in overnight gill net sets; gametes from five females and 21 males were stripped, and eggs were immediately fertilized. The embyros were then separated into one of 12 incubation boxes (each approximated 0.2 m^2) fitted with synthetic grass. Six boxes each were transferred to Blea Water (54.489, −2.852) and Small Water (54.483, −2.843) within 24 h. Within these refuge lakes, the boxes were installed only about 5 m offshore at a depth of around 0.7 m and secured to prevent movement during possible wave actions during the next 4 months of incubation. Although only about 24,000 embyros were estimated to be translocated to each lake, juvenile whitefish were sampled during that year of translocation from Blea Water (Winfield *et al.*, 1997) and later monitoring provided evidence of wild reproduction in both refuge waters (Winfield et al., 2003; Winfield *et al.*, 2013a).

Translocation has also been attempted as a conservation strategy for *C. albula*, which are more endangered in the British Isles than *C. lavaretus*, given that *C. albula* historically occurred in only two water bodies in Scotland and two water bodies in England (Maitland and Lyle, 1990; Winfield *et al.*, 2012; Bean *et al.*, 2016; Lyle *et al.*, 2019). *C. albula* has been extirpated from Scottish waters since the 1970s, however (Maitland, 2007), and was declared extirpated from Bassenthwaite Lake (54.650, −3.214) in England after extensive surveys failed to yield one fish during 2007-2008 (Winfield *et al.*, 2008). Prior to the extirpation, however, initial refuge populations were attempted into two Scottish water bodies in 1988 (Maitland and Lyle, 1990), but those efforts failed (Winfield *et al.*, 2012). A later attempt to create a refuge population in two more Scottish water bodies via translocation of embryos and larvae was undertaken in 1997 and 1999; a viable population was subsequently created in one (*i.e.*, Loch Skeen (55.435, −3.311)), such that the Bassenthwaite population now lives on in a new water body (Winfield *et al.*, 2012). In all these translocation efforts to conserve *C. albula*, Winfield *et al.* (2012) noted that they avoided "...the use of hatcheries completely or limited their use to vendace development only to eyed-egg or swim-up larvae stages to guard against any inadvertent but significant genetic selection which is almost inevitable if older life stages are retained in captivity."

Outside of the purposes of conservation or restoration, our review also revealed widespread use of translocations throughout Europe for the purposes of creating or enhancing fisheries. For example, the translocations of age-0, age-1, and age-2 *C. albula* have been very common in Finland, although success was relatively low owing to high transport mortality (see Jurvelius *et al.*, 1995; Huuskonen *et al.*, 2004). Likewise, in Switzerland, translocations were common for fishery interests for more than a century (*e.g.*, Steinmann, 1950; Svarvar and Müller, 1982) until the practice was federally banned in 1991 (BGF 6 1 b; https://www.fedlex.admin.ch/eli/cc/1991/2259_2259_2259/de) after realizing that translocations led to introgressions with locally adapted whitefish populations or endangerment of other native species. One Swiss case study, however, is worth noting. Whitefish species from Lake Zug (47.132, 8.485) were translocated to non-whitefish lakes, including Lake Maggiore (46.135, 8.768) and Lake Lugano (45.991, 8.970) at the beginning of the 20th century for the purposes of creating whitefish fisheries. Yet decades later the three whitefish species in Lake Zug either became extinct or survived as an introgressed species (*e.g.*, *C. supersum*, Selz and Seehausen, 2023). Hudson *et al.* (2011) revealed that the populations of whitefish that are present in lakes Maggiore and Lugano group in a neighbor-joining tree with the extant population of whitefish from Lake Zug. Thus, ironically, the historically translocated whitefish from Lake Zug into lakes Maggiore and Lugano may be important – albeit possibly introgressed- conservation units in Switzerland today.

Our review revealed that translocation can be an effective restoration or conservation tool, but that it has been rarely used for this purpose. Given how commonly it has been used in Europe for both conservation and fishery supplementation purposes, the methods for this strategy are likely relatively well developed and could easily be transferred to other regions such as North America where it has been far less commonly used. One key step to evaluate prior to undertaking translocation, however, is confirming that the recipient ecosystem can likely support survival for all life stages of the translocated species (sensu Adams *et al.*, 2014).

4 Habitat restoration

A diversity of habitat restoration strategies was identified in our review. Broadly speaking, we categorized them as to whether they targeted improving spawning habitat, improving connectivity, or targeting nutrients to improve oxygen, primary or even secondary production. Either directly or indirectly improving spawning habitat was the most common target strategy. In fact, the diversity of coregonines in North America, Europe, and Asia likely arose and was maintained owing to habitat complexity that facilitated differences in spawning habitats (*e.g.*, depths, tributaries) and timing (*e.g.*, Koelz, 1929; Smirnov, 1992; Vonlanthen *et al.*, 2012). Anthropogenic stressors have reduced the quality and/or quantity of coregonine spawning habitat across continents. For example, efforts to conserve *C. albula* in Bassenthwaite Lake were negatively affected by high levels of sedimentation that reduced egg survival (Winfield *et al.*, 2012). Artificial spawning substrates were developed to overcome this impediment, but continued inputs of winter sediments led to the eventual abandonment of this approach (Winfield *et al.*, 2006). Another stressor to nearshore coregonine spawning habitat in reservoirs has been steep winter drawdowns that expose optimal spawning habitat. To ameliorate this potential bottleneck, new spawning habitat (7.75 m^2 plots of artificial grass) that could be moved to deeper depths during a drawdown was placed in known spawning regions for *C. lavaretus* in Haweswater (Winfield *et al.*, 2002). Although eggs were recorded on the experimental plots for over a month, unusually high rainfall precluded the need to move the eggs in response to a drawdown, so the method was not fully tested. Winfield *et al.* (2002) described additional plans to deploy this technique at a larger scale but it has not yet occurred to date. Winfield *et al.* (2013a) also described how reservoir managers modified their hydrological regimes to benefit *C. lavaretus* reproduction, but there was no evidence that this effort ever improved recruitment. Finally, there were widespread efforts in Swiss lakes to introduce gravel substrates for lithophilic spawners and they were documented to benefit *S. alpinus* (*e.g.*, Ruhlé, 1977), but also likely benefitted coregonines.

Beyond the smaller scale habitat improvements described above, we also found two examples of reef construction designed to benefit coregonine spawning habitat in North America. In Bear Lake (U.S.: 40.846, −110.399) four rocky reefs (each covering about 100 m^2, with 153 m^3 of rock) were constructed in 10 m of water to enhance spawning habitat and recruitment of three endemic *Prosopium* spp. (Tolentino and Moon, 2012). The motivation was to provide additional deeper spawning habitat because shallower spawning habitats were commonly exposed during drought years, and initial evaluation revealed that all three species used the reefs for spawning (Tolentino and Moon 2012). In the Detroit River (Canada and U.S.: 42.191, −83.132), nearly 6000 ha of cobble and bedrock was lost as a result of construction of shipping channels and dredge spoil dumping more than a century ago (Bennion and Manny, 2011). Given that removal of the substrate has been hypothesized to limit the recovery of several lithophilic species, include *C. clupeaformis* (Mitchill; Lake whitefish) within this river system (Hondorp *et al.*, 2014), seven rock reefs were constructed near areas documented to be historically important for spawning, totaling more than 50,000 m^2 (Manny *et al.*, 2015; Vaccaro *et al.*, 2016; Fischer *et al.*, 2018). Evaluation of whether the reefs increased egg deposition relative to elsewhere revealed no increase for *C. clupeaformis*, but higher deposition for other species (*e.g.*, *Acipenser fulvescens* Rafinesque; Lake Sturgeon, Fischer *et al.*, 2018). Hydrodynamics (*e.g.*, currents and velocity) in addition to variables like depth and substrate likely play a key role for coregonine spawning habitat selection (Lahti *et al.*, 1979; Zuromska, 1982; Meng and Müller, 1988; Ventling-Schwank and Livingstone, 1994; Weidel *et al.*, 2023), indicating the importance of baseline understanding of key habitat characteristics prior to determining how best to invest in spawning habitat creation or amelioration.

Ensuring connectivity between critical habitats is a common conservation strategy for many different taxa (Moilanen *et al.*, 2005; Magris *et al.*, 2018). For coregonines, Hondorp *et al.* (2014) described the importance of understanding whether there was sufficient connectivity between spawning and nursery habitats for *C. clupeaformis* larvae in the Detroit River. In the Arctic, Leppi *et al.* (2023) likewise speculated as to how climate change could affect the connectivity of several key habitats for migratory *C. nasus* (Pallas; Broad Whitefish). Kiffney *et al.* (2018) described how *P. williamsoni* (Girard; Mountain Whitefish) exploited a newly installed fishway on the Cedar River (U.S.: 47.374, −121.970) to colonize habitat at least 15 km above the dam (Kiffney *et al.*, 2018). Even though *P. williamsoni* was not the intended beneficiary, the study demonstrates how large coregonines can take advantage of passage opportunities designed for salmon and trout. Finally, the *C. huntsmani* recovery plan included the completion of a new fish passage facility to allow access into the upper Petite Lakes (44.343, −64.566), which are presumed to possess critical spawning habitat (Fisheries and Oceans Canada, 2018).

One final tool that has been used to restore or conserve coregonine habitat is nutrient management. Across the broad distribution of coregonines, natural resource management policies differ such that in some jurisdictions, nutrient management is under the purview of a non-fisheries authority (*i.e.*, water quality managers) whereas in other cases fishery managers can regulate nutrient inputs. There are several examples in both North America and Europe where benthic fish habitat has improved because of land or water policies that have sought to improve oxygen concentrations in the lake (Ludsin *et al.*, 2001; Wanzenböck *et al.*, 2002, Vonlanthen *et al.*, 2012). In Switzerland, for example, hypoxic waters have been ameliorated by diffusing oxygen over the bottom of the lake during the growing season and then using compressed air to improve vertical circulation and bring oxygen deficient deepwater to the surface where it can more easily absorb oxygen during the winter months (see Gächter, 1987; Vonlanthen *et al.*, 2019). This approach has benefitted many fish species, including whitefishes. Below, however, we describe specific examples where scientists or fishery managers have sought to alter nutrient inputs for the direct benefit of coregonines.

In the U.K., eutrophication has not only threatened both *C. lavaretus* and *C. albula*, but also cited as a cause of the local extinction of the only two native populations of *C. albula* in Scotland (Maitland and Lyle, 2013). In Wales, one strategy to conserve *C. lavaretus* in Llyn Tegid was to reduce nutrient inputs by altering farming practices within two tributaries (Owens *et al.*, 2006). Likewise, in England, a strategy to conserve *C. albula* in Bassenthwaite Lake involved improving the capacity of a local upstream sewage treatment facility to remove phosphorus and ideally improve egg survival (Winfield *et al.*, 2012). In Hamilton Harbor (43.285, −79.851) in Lake Ontario, a Remedial Action Plan has been developed that includes a goal to improve dissolved oxygen based on the needs of *C. artedi* (Bowlby *et al.*, 2016). In the U. S. state of Minnesota, a model was developed to identify which lakes were sufficiently deep and of current good water quality to sustain *C. artedi*, even with warming climate scenarios (Fang *et al.*, 2012; Jacobson *et al.*, 2013). To maintain the water quality in these so-called "refuge" lakes for *C. artedi*, however, several different agencies have collaborated to protect 75% of the watershed from agricultural or urban development (Paukert *et al.*, 2016) and this target has been achieved for three of those previously identified refuge lakes (P. Jacobson, personal communication, January 5, 2024). Although most efforts to improve coregonine habitat have involved the reduction of nutrient inputs, one example was also identified where aquatic habitat was fertilized to enhance fish production. Hardy *et al.* (2022) describe the application of ammonium polyphosphate over a 20-km stretch of the Kootenai River (U.S.: 48.620, −116.049) because the habitat below the dam had become ultra-oligotrophic following the dam construction. *P. williamsoni* was one of several species that increased in abundance and biomass in response to the fertilization, likely owing to increased primary and secondary production to support improved its recruitment (Hardy *et al.*, 2022).

5 Eliminating harvest or creation of protected areas

A common strategy to reduce mortality among imperiled fish populations or populations that are being reintroduced is to reduce fishing mortality (Walters and Martell, 2004). Among coregonine populations, there are several examples of regulating harvest to manage or sustain fisheries (*e.g.*, Nümann, 1972; Gassner *et al.*, 2004; Ebener *et al.*, 2008), but we found relatively few examples of eliminating harvest altogether or creating a "protected area" (akin to a marine protected area where fish are protected from harvest) in a conservation or restoration context. Lake Constance is an excellent case study of altering harvest regulations through time. There are three whitefish species in Lake Constance targeted by local fisheries and they have undergone dramatic changes in abundance over time, largely corresponding with changing trophic conditions from oligotrophic (1900–1955) to mesotrophic (1955–1965) to eutrophic (1965–1990) to mesotrophic (1990–2005) and finally back to oligotrophic (2005-present); the highest yield occurred during the most recent mesotrophic phase (Baer *et al.*, 2017). Nutrient management and fisheries management are decoupled in the Lake Constance watershed, and the strict controls on nutrient inputs (Baer *et al.*, 2017) coupled with the negative impacts of invasive *Dreissena bugensis* (Andrusov; Quagga mussel) and *Gasterosteus aculeatus* (Linnaeus; Threespine stickleback) on whitefishes (Rösch *et al.*, 2018) have reduced whitefish population abundance to near unprecedented low levels. As a result, the interagency fisheries management group recently imposed a 3 yr ban on using nets and fish hooks to harvest whitefish, beginning in 2024 (see https://ibkf.org/pressemitteilungen/; accessed 10 August 2023). The next decade or so in Lake Constance will reveal whether fishery closures are sufficient to conserve imperiled populations already experiencing multiple stressors. Lake Lucerne (47.018, 8.408) in Switzerland offers another case study of a fishery closure to conserve an imperiled coregonine population. *C. nobilis* (Haack; Edelfisch) was historically the second most abundant whitefish species in the lake prior to succumbing first to high fishing pressure and then second to eutrophication (Vonlanthen *et al.*, 2012) and was even believed to be extinct by the 1980s prior to being rediscovered in the 2000s (Müller, 2007). Since this time, *C. nobilis* has been afforded protection from the fishery year-round to help sustain its recovery (Selz and Seehausen, 2023).

We found two other case studies where a coregonine fishery was closed in response to low population abundance. The first was the *C. albula* fishery in the Estonian waters of Lake Peipsi (58.667, 27.296) from 2000-2006 (Kangur *et al.*, 2020). When environmental conditions improved, a lower level of harvest was resumed but the population is still low enough that it is subject to future closures to sustain the population (K. Kangur, personal communication, September 14, 2023). The only other documented closure that we found was from Lake Michigan in the 1970s. The deepwater cisco assemblage had collapsed from a once diverse group of 8 species down to only 1 – *C. hoyi*, which was the smallest species in the former assemblage (Smith, 1964; Wells and McLain, 1973). By the early 1970s, even *C. hoyi* yield had dropped to near record-low levels (Brown *et al.*, 1985). By 1976, a commercial fishing closure was approved after overcoming legal challenges, but it was relatively short-lived with an interagency technical committee recommending a return to lower levels of fishing by 1978 (Brown *et al.*, 1985). Over the next several years, *C. hoyi* recruitment reached record levels and led to high levels of population abundance in subsequent fisheries independent assessments, although the commercial fishery yields never recovered to levels that were once attained in the 1960s likely owing to changing market conditions (Bunnell *et al.*, 2006). With these two case studies, it appears that the closure of coregonine fisheries can contribute to a population recovery. Use of this management action is certainly within the realm of traditional fishery management strategies that could be used for future conservation or restoration efforts.

The designation of protected areas or reserves have become another fishery management tool, particularly in marine ecosystems, to protect both fish and their habitat from the potential negative effects of fishing (*e.g.*, Agardy, 1997; Gill *et al.*, 2017). Protected areas, however, are less commonly used in freshwater ecosystems than in marine ones (Saunders *et al.*, 2002), and we found only a few examples of creating protected areas to directly benefit coregonine species. Even so,

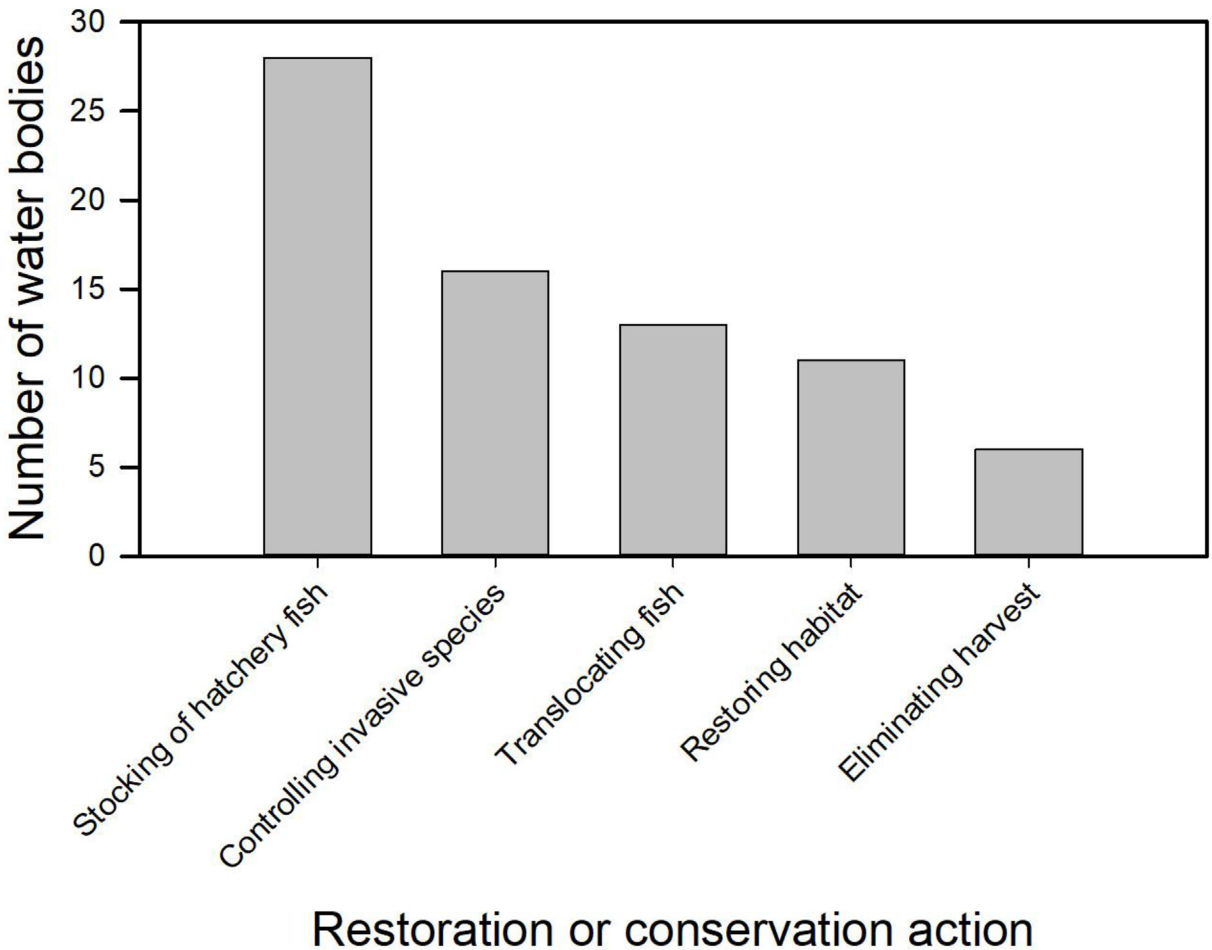

Fig. 1. The number of water bodies in which we documented a given targeted restoration or conservation action for coregonines during our review. Note that stocking of hatchery-reared fish did not include water bodies where the primary short-term objective was the supplementation or creation of fisheries.

one advantage of creating a protected area is that multiple species can benefit. In the Lake Superior (U.S., Canada: 47.921, −87.411), for example, coregonines benefitted from no-take protected areas that were designed to restore and conserve *Salvelinus namaycush* (Walbaum; Lake trout; see Zuccarino-Crowe *et al.*, 2016; Dray Carl, Wisconsin Department of Natural Resources, personal communication, February 27, 2024). Another illustrative case study is in Sweden, where more than 205 lakes have been reported to have some area closed to fishing at least part of the year. Sandström *et al.* (2016) surveyed these lakes and found that they generally occupied relatively small surface areas (*e.g.*, 1.6% of the lake, on average) and only rarely was fishing banned throughout the year, with *Salmo trutta* (Linnaeus; Trout) typically the focal species. An exception was in Lake Vättern (58.322, 14.501), where a reserve has been in place since 2005 and protects at least 16% of the lake surface area, with protecting whitefish stocks identified as one of the target conservation goals (Sandström *et al.*, 2016). A second example of creating a protected area specifically for coregonines occurred in a coastal region (∼ 61.127, 17.303) of the Gulf of Bothnia in the northern Baltic Sea. In 2011, both a no-take reserve of 147 km^2 and an even larger seasonal closure during the spawning period were established to protect sea-spawning *C. maraena*. Bergström *et al.* (2022) summarized the results of monitoring adult densities during the late fall spawning season and young-of-year (YOY) fishes in the spring. They reported significant increases in adult densities in both protected areas relative to reference areas during 2011–2016, but no increase in YOY abundance. When the no-take reserve was reopened to fishing in 2016, however, annual monitoring through 2021 revealed declines in catch per unit effort in the former protected areas and no differences in densities from the reference areas. Bergström *et al.* (2022) concluded that *C. maraena* responded quickly and positively to the protected areas, but that those positive effects can quickly be lost once restrictions are lifted. Although there is limited knowledge regarding the effectiveness of creating protected areas for coregonines, the potential positive benefits that this management tool has exhibited for other fish species (*e.g.*, Gill *et al.*, 2017) suggests it could also

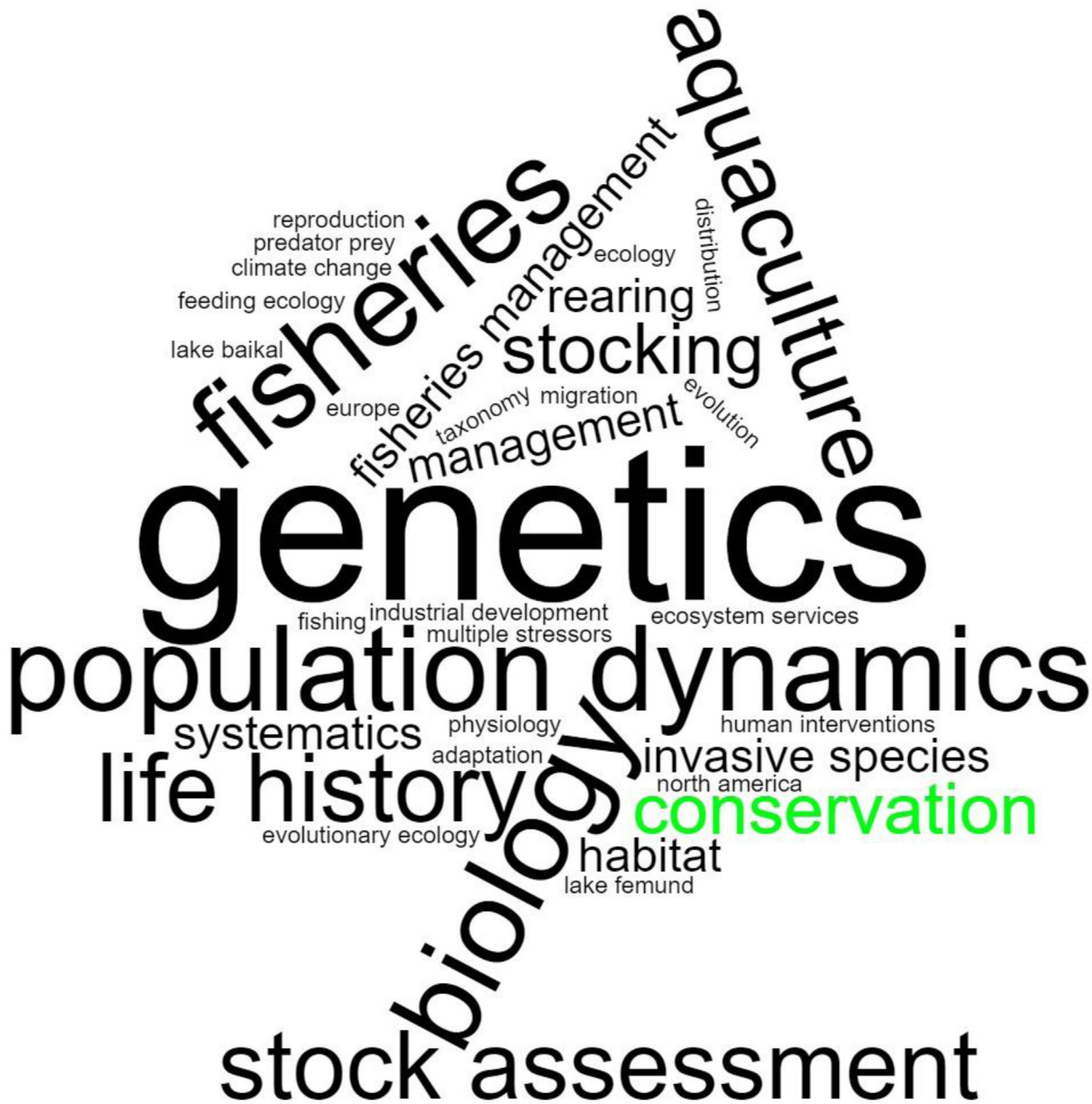

Fig. 2. "Wordcloud" (generated using www.wordclouds.com) based on the theme area words or phrases that have organized the proceedings of the 10 Coregonid Symposia that have been published since 1995. The size of the word or phrases is positively related to the frequency that the word was used (*e.g.*, genetics was used the most, $N=9$). Conservation ($N=3$) is highlighted with green to show that the word has been relatively rarely used as a theme area in recently published proceedings.

be an effective conservation or restoration tool for whitefishes and ciscoes.

6 Control of invasive species

Invasive species have been identified as a threat or stressor to coregonine populations across their distribution (*e.g.*, Adams and Maitland, 1998; Winfield *et al.*, 1998; Hrabik *et al.*, 1998; Etheridge *et al.*, 2011; Wood, 2016; DeWeber *et al.*, 2022). Even if resources are available, controlling invasive species can often be challenging (Simberloff, 2013), especially those that have high reproductive output or wide physiological tolerance (*e.g.*, Marchetti *et al.*, 2004). In aquatic ecosystems, there are examples of intensive invasive species control to protect fish and fisheries, including invasive *Petromyzon marinus* (Linnaeus; Sea Lamprey) control to protect salmonine fisheries in the Laurentian Great Lakes (Christie and Goddard, 2003) or the concerted effort to suppress invasive *S. namaycush* in Yellowstone Lake (U.S.: 44.456, −110.340) to protect endemic *Oncorhynchus clarkii bouvieri* (Jordan and Gilbert; Cutthroat trout; Koel *et al.*, 2020). In our review, we also found several examples describing some level of effort to reduce the impacts of invasive species on imperiled coregonine populations.

Conservation efforts to reduce invasive species impacts on coregonines have ranged from exploratory modeling to preventative legislation to intensive control through the applications of chemicals or physical removal. For example, Conley *et al.* (2021) modeled the potential effectiveness of applying rotenone chemical treatments to water bodies in the Adirondack region (U.S.) to eradicate them of potential competitors or predators of *P. cylindraceum*, when the other physical and chemical habitat was otherwise viable (see Conley *et al.*, 2021). In England, the use of live baits was banned in 14 lakes in 2002 to protect threatened coregonines (*e.g.*, *C. albula*, *C. lavaretus*) and *S. alpinus* from further spread of potentially harmful invasive species (Winfield and Durie, 2004). In Nova Scotia, Canada, one of the exploratory recovery actions to conserve *C. huntsmani* was electrofishing to reduce the densities of invasive piscivores, although the effectiveness of the program has not yet been reported (Fisheries and Oceans Canada, 2018). Finally, a more intensive control effort was undertaken in Lake Päijänne (Finland: 61.662, 25.504) where less desirable percids and cyprinids were targeted for removal to improve the survival of production and survival of larval coregonines (Urpanen *et al.*, 2012). Although most of the fish species that were removed from this 15,700 ha lake were native, they were perceived to be detrimental to the diminishing coregonine assemblage. Nonetheless, with a before-after-control-impact design, no positive effect of the removal was detected on the larval coregonines in the 5 yr after the 4 yr of intensive removal (Urpanen *et al.*, 2012). Finally, in Lake Constance, scientists and managers are speculating possible strategies to control invasive *D. bugensis* and *G. aculeatus* that are hypothesized to be contributing to the declining whitefish populations. For example, fishery managers could consider actions aimed at boosting the densities of existing molluscivorous fishes in the lake to reduce *D. bugensis* densities (Baer *et al.*, 2022), although any biomanipulation effort can still lead to unexpected outcomes (Jeppesen *et al.*, 2012). Likewise, scientists have already begun evaluating the efficacy of different techniques (*e.g.*, fall trawling at depths 9-12 m) to remove high densities of *G. aculeatus* (Gugele *et al.*, 2020). Although controlling invasive species can be extremely challenging, our review revealed relatively widespread interest across both North America and Europe in researching and developing techniques that could be feasible in the future. At the same time, we were unable to document any examples where managers have sought to control invasive species for the direct benefit of coregonines and been successful, to date.

7 Conclusions

Our review revealed a diversity of management actions that have been used to restore or conserve coregonines across their wide distribution. Although we acknowledge our review was assuredly incomplete given that some efforts were likely not reported or easily accessible based on our collection methods, we counted the frequency of water bodies for which each coregonine restoration or conservation strategy was applied ($N = 74$ total). Our estimates of how commonly each strategy was used, illustrated that stocking of hatchery-reared fish was the most frequent ($N = 28$, 38% of all strategies, Fig. 1), which perhaps is not surprising given how commonly fishery managers have exploited stocking of hatchery-reared coregonines for other purposes such as fishery supplementation. Even in this review, we scrutinized several case studies to come to the sometimes-difficult decision of the primary objective of the stocking. Regardless, we note this relatively high frequency of stocking was skewed by the inclusion of 24 water bodies in New York (U.S.) where *P. cylindraceum* were stocked for the purposes of reintroduction. One explanation for stocking of hatchery-reared fish being not even more frequently documented for conservation purposes is legitimate genetic concerns about stocking hatchery reared fish in the same water body as imperiled populations (see Flagg and Nash, 1999; McMillan *et al.*, 2023). At the same time, the use of hatchery-reared fish will likely continue to be a critical component of restoration efforts where reintroduction of a coregonine species is the primary objective, as was the case for *P. cylindraceum* in Adirondack water bodies, *C. oxyrinchus* in the Rhine River, or *C. hoyi* in Lake Ontario.

The second most frequent ($N = 16$, 22%, Fig. 1) conservation or restoration strategy that we found was controlling invasive species to benefit coregonines. Given the widespread prevalence of non-indigenous species affecting aquatic ecosystems (Walsh *et al.*, 2016; Reynolds and Aldridge, 2021), it is not surprising that they can be stressor to sustaining coregonine populations. At the same time, the relatively high frequency was skewed by the inclusion of 14 lakes in the U.K. where live baits were banned to protect threatened coregonine populations (Winfield and Durie, 2004). This more preventative measure requires much less effort than more active control measures that were reviewed, such as targeted electrofishing or trawling to remove unwanted invasive fishes (*e.g.*, Fisheries and Oceans, 2018; Gugele *et al.*, 2020).

The next most frequent strategies were translocations ($N = 13$, 17%) and habitat restoration ($N = 11$; 15%). Using translocations to conserve or restore coregonines was documented only in lakes in the U.K., and the primary purpose was to create "refuge" populations in cases where populations were threatened in their native water bodies and were translocated to nearby water bodies to reduce the chances of regional extirpation. Several success stories were documented, including successful translocation of *C. lavaretus* into several Scottish, English, and Welsh water bodies (see Etheridge *et al.*, 2010; Winfield *et al.*, 2008; Winfield *et al.*, 2013b; Winfield *et al.*, 2013c, Crotti *et al.*, 2021b). Given that translocations have also been commonly deployed in other European countries to support fisheries (*e.g.*, Jurvelius *et al.*, 1995), translocation methods are sufficiently developed and could be transferred to other regions with limited use of this strategy, such as North America where there are ongoing attempts to reintroduce coregonines into the lakes where they have been extirpated (see Bunnell *et al.*, 2023). Examples of habitat restoration were documented across several countries and in both riverine and lake habitats. For the studies where new spawning habitat was created, there was documentation of coregonines quickly exploiting this new resource (*e.g.*, Winfield *et al.*, 2002; Tolentino and Moon, 2012). Broadly speaking, investing resources on habitat restoration that can allow fishes to overcome critical bottlenecks in their life history may ultimately outperform other strategies that require annual investment to sustain or enhance fish populations (*e.g.*, Sass *et al.*, 2017; Radinger *et al.*, 2023). Hence, one key consideration for managers that are considering habitat restoration as a conservation or restoration strategy is to first identify critical habitat that has been degraded to maximize the probability that investment to improve or create comparable critical habitat will, indeed, lead to long term returns in higher population densities.

Imposing strict harvest regulations or the creation of protected areas was found in 6 lakes (*i.e.*, 8%). That this number was not higher was somewhat surprising, especially given that managing harvest is a relatively common action for managers to use in fisheries. Hence, we suspect that there may be more examples of fishery closures to protect imperiled populations than we documented through our methods. The creation of protected areas, however, to explicitly protect imperiled coregonine species from fishing mortality was only documented in two areas (see Sandström *et al.*, 2016; Bergström *et al.*, 2022) and only one of them was in freshwater. Broadly speaking, the use of reserves to protect freshwater or estuarine fish populations has lagged the usage for marine fish populations (Saunders *et al.*, 2002). At the global policy level, momentum is growing towards attaining ambitious goals such as ensuring that 30% of the Earth's "degraded terrestrial, inland water, and marine and coastal ecosystems are under effective restoration" by 2030 (Convention on Biological Diversity, 2022). Hence the creation of freshwater reserves for broader ecosystem benefits (*e.g.*, protecting habitat and broader biodiversity) may become increasingly frequent in the coming decade and could provide a leveraging opportunity for fishery managers targeting conservation or restoration of coregonines.

In conclusion, this review revealed that the documentation of conservation or restoration strategies targeting coregonine species is not as well documented as one might have predicted given the stressors that they are enduring or the extirpations and extinctions that have occurred. One possible explanation is that coregonines are not as commonly the focus of conservation or restoration relative to other salmon or trout in the Salmonidae family (see existing books or reviews on salmon restoration: Verspoor *et al.*, 2007; Naish *et al.*, 2007; de Leaniz *et al.*, 2007), but it is possible that coregonines still indirectly benefit from restoration efforts targeting other species in their same family. For example, a review of restoration projects in the national Swedish database indicated more than 2000 projects, but only 0.2% noted coregonines as the target species (unpublished data). In fact, our best examples of targeted restoration or conservation was in the U.K., where coregonines are rare and where legislative protection has undoubtedly spurred action. Another indicator of the limited focus on restoration or conservation even within the coregonine scientific community was the review of the theme area names that have organized the proceedings of the 10 Coregonid Symposia that have been published since 1995 (the symposia proceedings published prior to 1995 did not organize papers into theme areas). Of the 36 words or phrases that were included in the wordcloud, genetics was the most common ($N = 9$), followed by "biology", "fisheries", and "population dynamics" (each with $N = 5$, Fig. 2). "Conservation" was only the 9th most common ($N = 3$) and "restoration" was never included in a theme area name, revealing the relatively small number of times that symposia papers have reported efforts related to coregonine conservation or restoration. Furthermore, the appearance of "conservation" first occurred in the 2008 symposium (Tallman *et al.*, 2012) and then reappeared in the 2011 (Wanzenböck and Winfield, 2013) and 2020 symposia (Karjalainen *et al.*, 2021). Given this increasing frequency, it appears that these topics are increasingly being studied and potentially implemented to the benefit of coregonine populations. Whether future symposia place even greater emphasis on conservation and restoration topics remains to be seen, but ideally this review will allow fishery scientists and managers to consider a broader diversity of restoration or conservation strategies when these objectives are prioritized.

Acknowledgements

We are thankful to the International Committee of the 2023 Coregonid Symposium for inviting this as a plenary presentation. We thank Katie Anweiler for her technical assistance with the manuscript and Dan Yule and two anonymous reviewers for their helpful comments that improved the paper. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. government.

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Cite this article as: Bunnell DB, Anneville O, Baer J, Bean CW, Kahilainen KK, Sandström A, Selz OM, Vonlanthen P, Wanzenböck J, Weidel BC. 2024. How diverse is the toolbox? A review of management actions to conserve or restore coregonines. *Int. J. Lim.* **60**: 5 :