







## Review Article

# The quest for successful Atlantic salmon restoration: perspectives, priorities, and maxims

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Atlantic salmon is often a focal species of restoration efforts throughout the north Atlantic and it is therefore an excellent case study for how best to design programmes to address and mitigate threats and correct population declines. This perspective is written to promote the work that has been accomplished towards restoration of Atlantic salmon populations and synthesize how we believe the lessons can be used effectively to support efforts by management agencies to restore populations. We reviewed where restoration is needed for Atlantic salmon, agreed on

definitions for three levels of successful restoration, and then applied these criteria to 49 published papers focused on Atlantic salmon restoration. We identified 16 successful examples of restoration among 49 papers reviewed and discussed what interventions led to success versus failure. We then addressed key questions about when hatchery stocking should be used as part of a restoration measure and whether local restoration efforts are enough when these wide-ranging species encounter broad-scale changes in the north Atlantic, specifically related to issues of climate change and to marine survival. We advise to avoid restoration as much as possible by protecting and managing existing populations and when restoration is necessary, problems should be identified and addressed in partnership with river users. With appropriate resources and research to resolve ongoing mysteries, restoration of lost Atlantic salmon populations is absolutely feasible.

**Keywords:** ecosystem services, remediation, restoration, salmonidae, success.

“Nay, the salmon is not lost; for pray take notice, no man can lose what he never had”—Izaak Walton (1654)

## Introduction

North America and Europe have thousands of rivers that historically had Atlantic salmon (*Salmo salar* L.) populations. Today, only a fraction of the historic strongholds still maintains wild populations and throughout much of its natural distribution, the species is considered to be at risk (WWF, 2001; ICES, 2020). Archeozoological records and historical market data revealed salmon population declines had been ongoing since the early Middle Ages (450 AD) and were linked to the rise of water mills, small hydropower, the blocking of spawning tributaries, and later damming, straightening, channelization, and pollution of large rivers (Lenders *et al.*, 2016). These population declines occurred despite the adoption of mitigation measures that were intended to protect the species (Dunfield, 1985; Lenders *et al.*, 2016). Already in 1215, the Magna Carta legislated the removal of weirs and dams that obstructed migrating salmon in English rivers. In North America, the depletion of Atlantic salmon by European colonists triggered treaties to prevent overexploitation of stocks in Quebec (Lower Canada; Nettle, 1857) and to halt (unsuccessfully) the extirpation of Lake Ontario’s stock of landlocked salmon (Huntsman, 1944).

The cumulative decline of salmon has been geographically widespread and is well documented. In Lake Ontario, the bountiful runs of Atlantic salmon that could initially be harvested by the boatful entirely disappeared by the end of the 19th century (Webster, 1982; Bogue, 2001). In Portugal, the southern limit of the species distribution in Europe, salmon abundance has declined by an estimated 90% from historic levels over the past 50–60 years (Cabral *et al.*, 2005). In the Rhine River, catches in the lower river during the late 19th century reached over 100000 individuals, but had dropped to zero within 50 years (Lenders *et al.*, 2016). Further, the southern extent of the North American range of the species shifted northward by 2° latitude by the early to mid-1800s with the extirpation of the southernmost USA populations (Fay *et al.*, 2006).

Restoration ecology is replete with efforts to reintroduce, recolonize, and/or replenish native fish stocks in the historic range (Hobbs and Harris, 2001; Zimmerman and Kruger, 2009) in order to return ecosystem and related cultural services of substantial value (Butler *et al.*, 2009; Childress *et al.*, 2014). Improvements to the quality and quantity of degraded habitat are generally the first and most critical steps to reestablish native fish stocks (Giller, 2005; Einum *et al.*, 2008). Many rivers have therefore undergone extensive work to undo damage resulting from habitat modification, pollution, dam building, and restriction of movement, siltation, eutrophication, channelization, acidification, and other human impacts that have contributed to the collapse or extirpation of fish stocks (Palmer *et al.*, 2005; Erkinaro *et al.*, 2011; Tummers *et al.*, 2016). At some sites, fish and river restoration programmes have been ongoing for

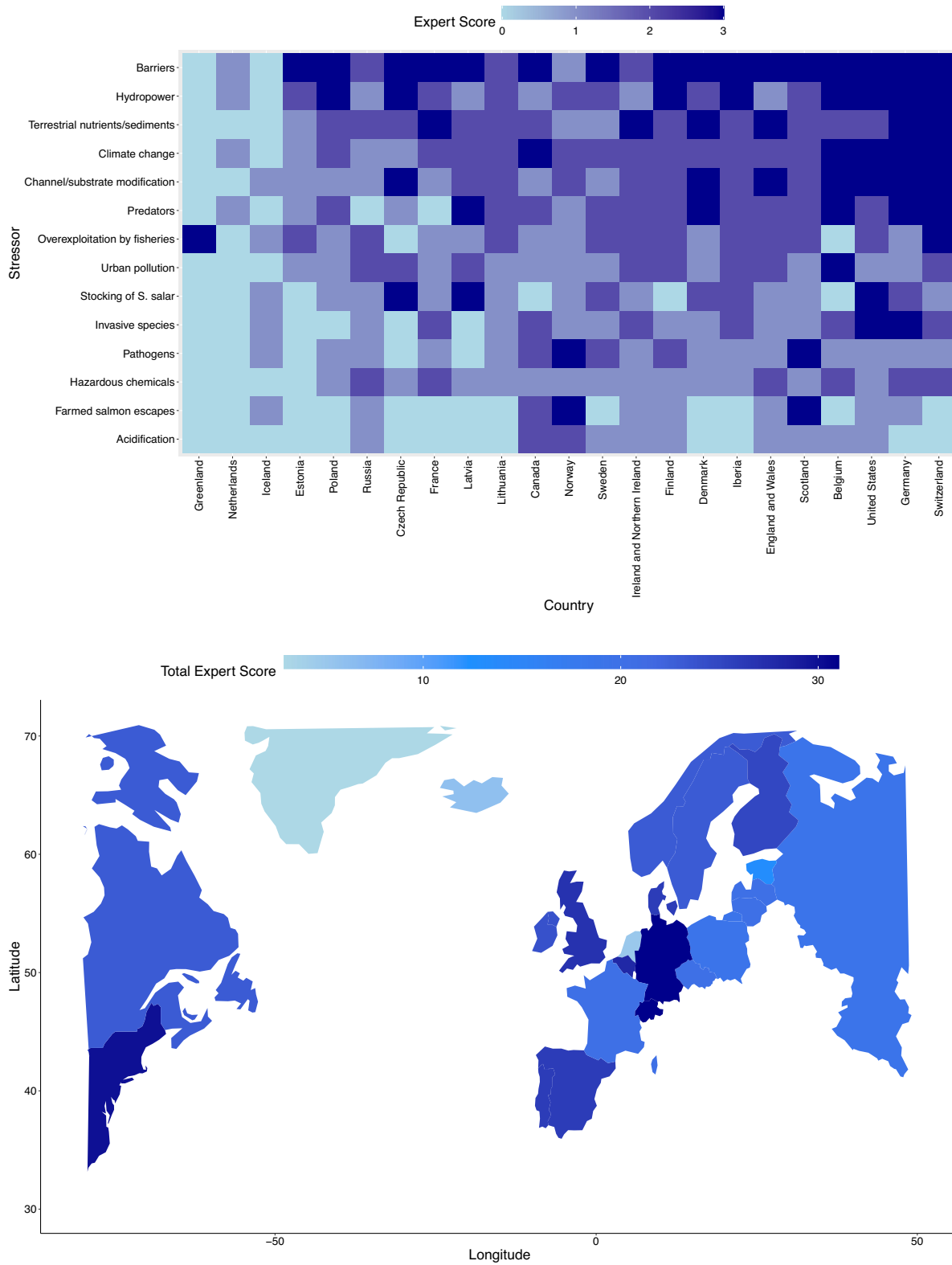
decades and new programmes continue to be implemented, as urgency in preserving or restoring species accelerates while stressors multiply. Stakeholders devote a large amount of limited resources every year to study and restore Atlantic salmon and related habitat, and this species presents an excellent case study for restoration ecology (Birnie-Gauvin *et al.*, 2018).

This perspective draws on the experience of an international team of experts that have worked on the restoration of Atlantic salmon in the fields of conservation genetics, ecology, physiology, behavioural sciences, fisheries biology, and ecoepidemiology, throughout the north Atlantic and Arctic range of Atlantic salmon. We start by reviewing how different stressors operate in different parts of the salmon’s distribution, continue with a discussion of how to define successful restoration action, and provide examples of success, failure, and unintended consequences of restoration. Finally, we review the controversial use of hatcheries for restoration, which we found to be a polarizing point of discussion when considering restoration issues throughout the range and the relative utility of local efforts in the face of ongoing global environmental change.

## In what situations is restoration needed?

Regional differences exist in the urgency of different threats to salmon, which guide evaluations of what the likely problems are that need to be addressed by a restoration programme. Although the ICES Working Group on Effectiveness of Recovery Actions for Atlantic Salmon carried out a ranking-based evaluation of the stressors limiting wild Atlantic salmon restoration, which generated detailed catchment-specific information (ICES, 2017a), it had only partial coverage across the species’ range. The evaluation was also broad with respect to some stressors. For example, the category “pollutants” (ICES, 2017a) can be divided into functional subtypes such as hazardous chemical substances, urban organic pollutants (e.g. sewage), excessive silt and nutrients, and acidification (Champion, 2003; Hesthagen *et al.*, 2011). To fill gaps and provide some prior information about the regionality of key challenges, we asked experts from 23 regions to rank the importance of 15 stressors to Atlantic salmon. Instructions were to provide an integer value from zero to three indicating zero, minor, moderate, or major impact of a stressor on salmon populations in a given region. For biogeographic convenience, Portugal and Spain were combined to “Iberia”; Ireland and Northern Ireland were combined; and England and Wales were combined. We were unfortunately unable to receive a response from a Russian representative, so we made an evaluation for this country based on North Atlantic Salmon Conservation Organization reports and expert inference from scientists familiar with the situation in Russia (Figure 1).

Switzerland and the United States ranked highest among nations for stressor scores, with a total score of 31 and 30, respectively, out of a possible total of 45 (15 categories multiplied by a maximum score of three). Greenland, The Netherlands, and Iceland scored



**Figure 1.** Expert assessments of the risks posed by 15 stressors to salmon populations in salmon-bearing regions. A small number of experts from each country contributed to the assessment and were asked to assign and integers from 0 (no threat) to 3 (major threat) to ordinal score the threat posed by each stressor. Scores are displayed for each country and each threat (top). Countries are sorted left to right from lowest to highest total score and stressors are sorted from bottom to top from lowest to highest total score. Summed scores are also displayed (bottom).

low at 3, 5, and 6, respectively. Migration barriers were the most urgent stressor, ranked everywhere except for Greenland (where there is only one river system with a population of Atlantic salmon) and Iceland. Acidification was regionally important in Norway and Canada. Norway, Canada, and Scotland are the main producers of farmed Atlantic salmon within the species' natural range and were the regions that scored high on impacts from escaped farmed salmon and pathogens from salmonid aquaculture (Figure 1). Some variation occurred among landlocked countries in how they ranked the stressor. Switzerland ranked highest whereas Czech Republic was eighth lowest on the ranking. In these countries, particularly urgent threats related to damming and river channelization were identified that, if remedied, could be immensely impactful for salmon restoration. Another interesting contrast was Belgium compared to the Netherlands. These neighbouring nations ranked third worst and second best, respectively, with the experts clearly perceiving the threats to their salmon populations differently. The management directives, river productivity, and other factors may change on small spatial scales, possibly causing such stark contrasts between nations. However, it might also reflect large individual differences in the perception of important impacts between experts. Our question sheet is included as an appendix (Appendix 1) and may be adapted to future efforts to score, rank, and prioritize restoration efforts for Atlantic salmon or other species at different scales.

### How can we evaluate salmon restoration initiatives?

The ultimate goal of restoration is to increase a population size to a biological reference point (Table 1) via natural reproduction, which can be defined in terms of genetic (e.g. effective population size; Horreo *et al.*, 2011a), reproductive (e.g. number of eggs deposited; Forseth *et al.*, 2013), demographic (e.g. carrying capacity), or social (e.g. harvestable surplus) conceptions of a sustainable population (Figure 2). Candidate metrics are used in different places to evaluate the past, present, and future status of a population, and changes to the population after restoration interventions can be used to establish whether efforts were successful. Restoration therefore requires knowledge of how many fish exist compared to how many are needed for a healthy population, which is the biological reference point. For Atlantic salmon, the biological reference point is often derived from the census number of adult spawners (Ferchaud *et al.*, 2016). The biological reference point for a river is ideally defined by historic abundance data or theoretical maximum suitable spawning area and egg deposition and perhaps adjusted to present environmental conditions, for example, if spawning grounds have been lost or water temperatures have changed such that historic baselines are no longer attainable. In the Swedish river Vindel, historic photos helped identify a reference state for the river and guide restoration objectives (Hellström *et al.*, 2019). Progress towards the biological reference point using census numbers can be tracked by counting large (i.e. not mature male parr, which are cryptic and impossible to visually identify) adults based on fishing catches, mark-recapture, counting fences/weirs/cameras, or spawning counts (fish seen breeding at spawning sites; Skoglund *et al.*, 2021). Because the definition of success is crucial for the evaluation of restoration, and no single definition meets the expectation of all stakeholders for salmon, we define success at three levels:

i) **Level 1 success: self-sustaining wild population:** Following restoration intervention (Table 1), the first level of success is

achieved if the population is self-sustaining in the absence of stocking. The population may remain small or depleted compared to historic levels, but the number of spawners would be expected to increase in subsequent years assuming that adequate habitat is available for reproduction. Small populations may be vulnerable to unforeseen perturbations and stochastic and changing environmental conditions that can undermine restoration efforts and push the population back below replacement levels (Palstra *et al.*, 2007), particularly due to variability in marine survival.

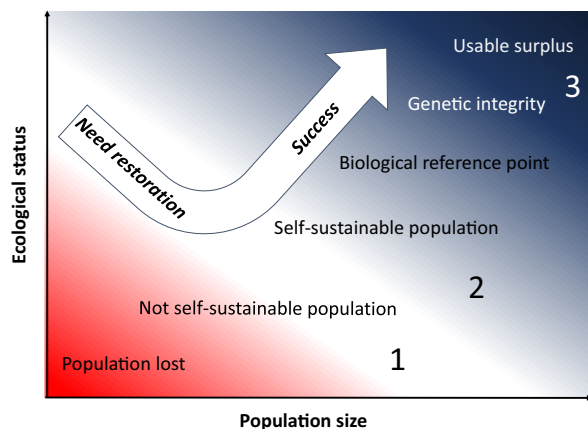
- ii) **Level 2 success: robust self-sustaining population:** The second level of success is reaching a population abundance level that reaches the biological reference point and is therefore sufficiently large such that the population remains resilient (self-sustaining) to environmental perturbations and variation. In restoration efforts, this level would presumably occur several years after interventions have finished and follow multiple years of increasing numbers towards or beyond the biological reference point established for the population. This level is often chosen as the objective of restoration projects and is monitored by census number with spawning counts or counting fences. In such populations, biological reference points may be achieved, but the number of breeders could still be suboptimal due to skewed sex ratios (Perrier *et al.*, 2016).
- iii) **Level 3 success: harvestable surplus:** Robust self-sustaining populations providing harvestable surplus beyond the biological reference point. Populations can be considered to have fully realized their potential following restoration when more spawners are returning than needed for replacement, yielding a harvestable surplus. In Norway and Canada, each salmon river is assigned a carrying capacity for the number of eggs needed to reach river-specific biological reference points, which quantifies the biological reference points targeted for attaining Level 2 and Level 3 success (O'Connell *et al.*, 1997; Forseth *et al.*, 2013). At this stage, the population is robust, and managers can set fishing quotas to remove part of the population down to a safe level and still allow to achieve complete replacement.

### Which restoration actions are successful?

To understand the success and evaluate failures of actions taken to restore Atlantic salmon populations, we conducted a focused literature search using the Web of Science search engine. The search covered all years up to the beginning of 2020 for TOPIC = atlantic salmon OR salmo salar AND TOPIC = restor\* OR remed\* to capture papers focusing on Atlantic salmon restoration. We acknowledge that this search would not capture potentially relevant papers focused on other salmonids or studies that did not include restoration in the topic of the paper (title, abstract, keywords), but we consider that our search yielded sufficient data for our analysis. The search yielded 681 results that were manually screened for relevance. Papers that did not focus on Atlantic salmon or did not attempt any intervention to investigate restoration were excluded. Additional papers were added by expert opinion and through the review of reference lists of the publications our search had missed, this effort resulted in 49 papers. Metadata from each study were extracted including the problem being investigated, the intervention being tested, and an evaluation of whether the intervention was successful or not at the three levels of success defined *a priori*.

**Table 1.** Glossary of key terms.

Term	Definition	Example
Intervention	Any action taken as part of a restoration programme that is intended to have a positive effect on the salmon biological reference point. Synonymous with a treatment, manipulation, or management action in a river.	Addition of spawning gravel is an intervention that may be used by managers to improve conditions for salmon spawning in a river.
Biological reference point	A quantitative measure of a salmon population, against which success of a restoration intervention is to be measured, relative to a baseline established prior to intervention. A biological reference point may be the number of spawners, the number of eggs deposited by females, or the effective population size.	Before and after addition of spawning gravel to a river, the census number of adult salmon is determined by spawning count to evaluate whether the intervention could be related to an increase in the census number, relative to a biological reference point.
Hatchery	A facility for controlled mating of broodstock salmon taken from the river (or sometimes a foreign stock) where eggs are planted in the gravel or reared to fry, parr, or smolt before release.	Broodstock male and female salmon are stored in hatchery tanks until gonads are ripe and then stripped of gametes to produce F1 offspring.
Gene bank	A specialized genetic repository and reproductive facility for evolutionarily enlightened artificial rearing of salmon. Gene banks harvest and store genetic material from salmon and supplement it annually to maintain genetic diversity. Offspring are produced from carefully selected genetic combinations of eggs and sperm to limit inbreeding depression and maximize genetic diversity. Gene banks may never be used but maintained if needed for replenishing threatened stocks.	During a concerning decline in a salmon population, genetic material is stored in a gene bank in case the population falls below a conservation limit. Gene banks are prudent to have in case of emergency and can be used to resupply a struggling population.
Conservation limit	A threshold used to establish whether a population is threatened with extinction. There are many possible conservation limits that may be used based on metrics such as spawning stock, eggs deposited, effective population size, etc. The limits may be conservative or liberal depending on the management risk tolerance level. The conservation limit lies somewhere below the biological reference point.	When a salmon population falls below the biological reference point, continued declines will eventually surpass the conservation limit that is used to trigger some action. The conservation limit should be conservative enough not to overreact to stochasticity, but not too conservative such that the population has approached extinction too rapidly to intervene or store genetic material in a gene bank.
Harvestable surplus	A harvestable surplus is a number or biomass of salmon beyond the biological reference point that can be harvested while allowing the population to still achieve replacement.	Level 3 success is achieved when the population exceeds the biological reference point and there is a harvestable surplus available to fisheries.



**Figure 2.** Illustration of successful Atlantic salmon restoration initiatives. Success levels correspond to our evaluation, with Level 1 indicating a self-sustaining population, Level 2 a robust self-sustaining population, and Level 3 a population with a harvestable surplus. Figure is based on data available in Table 2.

We present a table of key examples of success and failure to restore Atlantic salmon populations (Table 2). Based on the 49 studies, we identified restoration projects in 95 salmon populations, of which 18 did not reach any level of success as defined above, 39 reached a self-sustaining wild population (Level 1), zero attained a robust self-sustaining wild population (Level 2), and 26 reached a population with harvestable surplus (Level 3); success was uncertain due to lacking information in 13 rivers from the 49 cases. The main method used in the rivers where restoration failed was hatchery supplementation (stocking) without addressing the threats that originally contributed to population decline. Methods used in rivers reaching Level 1 (self-sustaining population) were habitat and water quality improvement, reconnection of river segments, and measures to eliminate the parasite *Gyrodactylus salaris*. In rivers reaching Level 3 (harvestable surplus), habitat and water quality improvement, dam removal, and liming were applied (Table 2; Figure 3). Among 19 papers reporting stocking Atlantic salmon, only two achieved any level of success; Saltveit *et al.* (2019) reported that catches in Suldalslagen, Norway were enhanced by stocking and Perrier *et al.*

**Table 2.** A review of Atlantic salmon restoration papers identified by a structured literature search and expert review revealed 49 relevant studies covering 95 rivers.

Article	Category	Problem	Intervention	Result	Explanation	Success	Populations (N)
Barlaup <i>et al.</i> (2008)	Habitat and water quality	Regulation of rivers impacts spawning habitats and recruitment	Addition of spawning gravel	Level 3 success; juvenile production can be enhanced by adding gravel to supply limited rivers	High spawning success (egg survival >80%), but gravel displacements due to floods	3	3
Champion (2003)	Habitat and water quality	Salmon population almost became extinct (negligible catches ~1940~1970) due to poor water quality in estuary and lower river due to untreated human sewage [biological oxygen demand (BOD) impact, low O <sub>2</sub> ] and due to intense industrial pollution cokerworks etc. (esp. ammonia, phenols, cyanide)	Industrial decline and cleanup of industrial effluent. Interceptor sewer system and sewage treatment for nearly 1M people in lower Tyne online 1980. Juvenile stocking (160K-360K fry/parr per year) commences due to Kielder dam in 1981	Level 3 success; the Tyne is now the best English salmon river with declared rod catch of adult salmon peaking at 5630 in 2011. Adult river stock est. 7000–18000 (2004–2016)	Predominant cause of strong recovery is concluded as due to pollution abatement and treatment actions. In early years of stocking, returning hatchery fish contributed 20% spawning, wild 80%. Declined as recolonization occurred	3	1
de Jong and Cowx (2016)	Habitat and water quality	Salmon habitat complexity lost in a Newfoundland river	Addition of boulder clusters, V-dams, and half-log covers	Level 3 success; sustained improvement in salmon abundance across 21 years	Increase of salmon density and biomass after structure addition and remaining high levels 20 years thereafter	3	1
Fjeldstad <i>et al.</i> (2012)	Connectivity and habitat quality	Habitat fragmentation, siltation, and habitat	Enhanced connectivity and improved sediment conditions after removal of two weirs	Level 3 success; spawning sites were re-created, pike and cyprinids were displaced, and juvenile density increased		3	1
Floyd <i>et al.</i> (2009)	Habitat and water quality	Decreased abundance of salmon and degraded habitats	Addition of artificial woody structures	Level 3 success; higher spawning densities in reaches with addition of woody debris	Presumably higher spawning densities improved overall salmon production	3	1
Hesthagen <i>et al.</i> (2011)	Habitat and water quality	Acidification of rivers	Liming programme	Level 3 success; increasing fish density, liming as important restoration factor of formerly acidified Norwegian rivers	More than 20 years of liming suggested for successful restoration of self-sustaining salmon populations in Norway	3	13
Koed <i>et al.</i> (2020)	Habitat and water quality	Declining populations of Atlantic salmon in Denmark	Habitat restorations, spawning ground additions, weir removals, fishing regulations/bans population genetics and barrier removals	Level 3 success; rehabilitation of salmon populations with significant increase in population densities	Success through multi-faceted management and focusing on several problems simultaneously	3	4
MacInnis <i>et al.</i> (2008)	Habitat and water quality	Habitat degradation seems to be driving poor salmon abundance	Create pools and shelter with woody debris	Level 3 success; exponential increase in spawning with sustained high levels in subsequent years		3	1
Saltveit <i>et al.</i> (2014)	Habitat and water quality	Water pollution and extirpation of Atlantic salmon in Akerselva, Norway	Water quality improvement programme via limitation of industrial discharges, pollution, and urban runoff into the river	Level 3 success; improved water quality and return of Atlantic salmon and sea trout to lower reaches	Further ecological improvement is limited due to several obstacles in urban environment	3	1
Calles and Greenberg (2005)	Connectivity and habitat quality	Power plant restricting passability	Construction of nature-like bypass channels	Level 1 success; salmon ascended the fishway to colonize upstream and descended as kelts to recondition at sea. Recolonization was, however, slower than expected	90–100% passage of fish that entered the fishways	1	1
De Jong <i>et al.</i> (1997)	Habitat and water quality	Decline in salmon abundance due to environmental perturbations	Three types of habitat improvements: boulder clusters, V-dams, and half-log covers and evaluation	Level 1 success; restoration led to increased habitat heterogeneity, habitat complexity, and salmon production and decreased competition	Boulder clusters were most effective as they increased densities of 0+, 1+ and 3+ juveniles, but also V-dams and half-log covers positively affected salmon	1	1
Hogg <i>et al.</i> (2015)	Connectivity and habitat quality	River connectivity reduced by dams and salmon population declining	Addition of new habitat following dam removal	Level 1 success; Increased density, biomass and diversity of fish assemblage upstream of dam removal	Multiple age classes of juvenile salmon abundant at all test sites after dam removal	1	1

Table 2. Continued

Article	Category	Problem	Intervention	Result	Explanation	Success	Populations (N)
Marttila <i>et al.</i> (2019)	Habitat and water quality	Channelization and removal of boulders reduced habitat complexity in 28 Finnish rivers	Instream structure added and connectivity to side channels restored	Level 1 success; young-of-the-year salmon increasing	Challenging to ascribe change in young of the year (YOY) densities directly to restoration efforts, but a good sign	1	28
Perrier <i>et al.</i> (2014)	Stocking/ fish passage	Erosion of genetic diversity in French salmon populations caused by fragmentation	Restoration of connectivity and stocking	Level 1 success; recolonization and reproduction of upstream areas from downstream habitats	Majority of genotyped individuals in recolonized sites originated from downstream areas, but also prominent share from more distant sites or hybrids	1	1
Saltveit <i>et al.</i> (2019)	Fish passage/ hydropower/ stocking	River Suldalslagen was regulated for hydropower, resulting in flow reduction, sedimentation, and carpet moss	New flow regime implemented to offset changes caused by regulation, stocking based on gene bank method	Level 1 success reached; Increase of catches of salmon >7 kg since 2010, but fishing and harvest based on stocking.	No pre-regulation data on fish catches known, hatchery fish contributed to increase of large salmon catches, no conclusion possible if goal of sustaining naturally reproducing wild large salmon has been achieved	1	1
Sandodden <i>et al.</i> (2018)	Biological invasions	Gyrodactylus parasite	Rotenone to kill salmon stock, eliminate invasive parasite, followed by reintroduction of native stock	Level 1 success: Gyrodactylus was eliminated and salmon were reintroduced	Reintroduction of native stocks in controlled removal of damaging invasive species is an extreme but effective measure when stocks face catastrophic mortality. Level 3 is supposed to be reached	1	6
Collins <i>et al.</i> (2010)	Habitat and water quality	Excessive sedimentation due to eroding channel banks	Evaluation of riparian fencing schemes to reduce siltation of salmon spawning gravel	Uncertain; riparian fencing schemes are recommended to reduce spawning site siltation, but no measure of effects on salmon production directly	Findings based on limited sample material and sample period, need follow up on how salmon production is affected	NA	1
Guyette <i>et al.</i> (2013)	Habitat and water quality	Decline in abundance and condition of juvenile salmon	Carcass analog nutrient addition with optimized timing for juvenile Atlantic salmon in headwater streams	Uncertain; increased growth of juvenile salmon and potential increased overwinter survival and younger smolt age, but unclear how this influences overall population production	Heavier individual mass and longer standard length in juvenile salmon at treatment sites compared to control reaches for 4 months after treatment	NA	1
Hill <i>et al.</i> (2019)	Fish passage/ hydropower	Migration of Lake Champlain salmon disconnected by dam	Removal of Willsboro dam in Boquet River, NY	Uncertain; rapid improvements in habitat quality after dam removal	Habitat improved, remains to be seen whether salmon production improves	NA	1
Hvidsten and Johnsen (1992)	Habitat and water quality	River Soya, Norway, was canalized for agricultural purposes, which affected the natural dynamic of sediment transport, reduced sediment granulometry and decreased the habitat quality for salmon juveniles	Several small weirs were built on these rivers, covering the riverbank and entire river bottom with blasted stones	Uncertain; population effect unclear. Restoration of the river bottom with blasted stones provided salmon with more substrate spaces. Densities of trout increased after the river bank was covered with stones	Sediments transported downstream from the canalized river stretch decreased the densities of juvenile salmon and trout	0	1
Izzo <i>et al.</i> (2016)	Fish passage/ hydropower	River connectivity reduced by dams and salmon population declining	Dam removal and installation of fish lifts	Uncertain; salmon easily passed sites where dams were removed but experienced prolonged delays at the fish lift	Need to investigate why passage was so poor at the fish lift	NA	1
Erkinaro <i>et al.</i> , 2011	Fish passage/ hydropower/ stocking	Historically renowned major salmon rivers have been harnessed for hydropower for 40–60 years without provisions for fish passage	Hydropower companies are obliged to compensate for the losses caused by dam construction by annual fish releases. Also, fishways were constructed in two rivers and more are planned to restore river connectivity	Uncertain; successful first years of the fishway operation with 150–500 salmon and trout annually entering the river provoked public pressure for restoring runs of fish. No actual results of the restoration success are available yet, although background investigations and pilot studies have been carried out or are underway	Projects have proved successful in bringing together authorities, hydropower companies, local organizations, and expertise from various institutions for a joint effort to tackle these multifaceted and multidisciplinary problems	NA	1

Table 2. Continued

Article	Category	Problem	Intervention	Result	Explanation	Success	Populations (N)
Jutila and Pruuki (1988)	Stocking	Decreasing wild production in Simojoki River	Stocking parr	Uncertain; smolt run increased but population effects not measured	Short-term benefits of stocking could not be extrapolated to restoration success (i.e. without further stocking) from the data presented	1	1
Kennedy et al. (2012)	Stocking	Decline of escapement	Stocking of 0 + fry to maintain recruitment near historical levels. Habitat degradation noted but not addressed	Uncertain; population effects unclear. Stocking of both unfed and fed-fry contributed to smolt production	Differences in the biological characteristics of wild vs. stocked salmon were noted and the fitness of offspring was questioned by authors. The long-term effect was not examined	0	1
Kennedy et al. (2014)	Habitat and water quality	Salmon disappearing in Northern Ireland	Installation of flow deflectors and boulder addition	Uncertain; increased juvenile salmon habitat with greater biomass of salmon on improved sites but fry recruitment unchanged	No change in overall salmon fry recruitment index, around 30% of boulders got buried by fine sediments and limited the efficacy	NA	1
McCarthy et al. (2009)	Habitat and water quality	Loss of spawning habitats due to hydropower development	Construction of a fish habitat compensation channel	Uncertain; population effects unclear. Successful mitigation of habitat loss may lead to improved salmon populations	Survey showed good habitat stability, a typical mean standing stock and verified spawning	NA	1
McLennan et al. (2019)	Habitat and water quality	Loss of migratory fish reduced nutrient subsidies and resulted in oligotrophication	Simulation of Atlantic salmon carcasses by deposition at the end of spawning period	Uncertain; quintupling of macroinvertebrate biomass compared to reference sites, faster growth of juvenile salmon and earlier smolt age	Positive effects on early life stages but does not report effects on spawning production	NA	1
Pedersen et al. (2007)	Habitat and water quality	Channelization, artificial draining, high nutrient loading to sea	Restoration of the river valley into a meandering river with wetlands, meadows and shallow lakes	Uncertain; enhanced biodiversity attributable to higher quality habitat. Total predation mortality increased due to colonization of birds, but overall salmon population confounded by hatchery release	Cormorants arrived in the newly restored area and increased the predation mortality of smolts	NA	1
Perrier et al. (2010)	Habitat and water quality	Migration barriers, canalization and degrading water quality in River Seine led to extinction of Atlantic salmon in the Seine River, France	No direct interventions to reestablish Atlantic salmon but progressive remediation of water quality	Uncertain; low number of spawners in a big river; Natural recolonization from long-distance straying and nearby stocked Atlantic salmon	Video counting of salmon in 2008 resulted in 162 individuals recolonizing the Seine	NA	1
Philippart et al. (1994)	Stocking	Extinction of Atlantic salmon due to pollution, weirs, and overexploitation	Evaluating the potential of salmon restoration via smolt production in tributaries, experimental stocking	Uncertain; promising results on re-establishment of salmon population, but remaining problems to be solved	Dense colonization of suitable habitats, promising survival and growth rates, smoltification and migration; but water quality and fish passes need to be improved	NA	1
Raastad et al. (1993)	Habitat and water quality	Regulation of rivers impacting survival and growth of young salmon	Habitat adjustment, building of rearing channel system, stocking, introducing dead organic material to enrich benthic fauna	Uncertain; increased density of macrobenthos and promising survival rate of young salmon	Preliminary results given at early stage of project; 30% survival of 1 + salmon	NA	1
Saavedra-Nieves et al. (2021)	Stocking/fish passage	Decline of salmon abundances in Ulla river due to fragmentation and low marine survival	Stocking actions, obstacle removal and fishway construction	Uncertain; Based on long-term dataset (1992–2018) from fish trap, a gradual population increase to the early 1990s was observed, then remained relatively stable until 2007 and increased thereafter due to an increase in the number of wild salmon entering the river	Increase in the number of returning salmon in the Ulla River achieved over this period is due to salmon stocking, the connectivity restoration in the river and to a higher marine survival rate.	0	1
Bacon et al. (2015)	Stocking	Decline of adult returns between 1966 and 1999. Presumed low over-winter ova survival and high within-cohort competition	Stock-recruit modelling of 33-year dataset to investigate whether ova-stocking programme led to more smolts being produced	Failure; ova-stocking failed to increase freshwater production	Separated effects of natural production and ova-stocking interventions using native stock fish	NA	NA



Table 2. Continued

Article	Category	Problem	Intervention	Result	Explanation	Success	Populations (N)
Bailey <i>et al.</i> (2010)	Stocking	Density dependent effects on populations	Stocking and tagging of fry and assessment of growth, survival, and movement in relation to density	Failure; Level 1 not reached. Density dependent effects were apparent on growth but not movement or mortality	Additional research needed to understand density effects of stocking	0	1
Barlaup <i>et al.</i> (2009)	Stocking	Decline in salmon due to acidification and hydropower development	Roe planting, restoration of spawning habitats, limited fishing for salmon	Failure; Level 1 not reached. Increased natural recruitment, but further measures needed for self maintaining population	Only about 10% natural recruitment	0	1
Bolscher <i>et al.</i> (2013)	Habitat and water quality, stocking	Extinction of Atlantic salmon in river Rhine	Rhine Action Plan for improvement of the Rhine river ecosystem and to reestablish salmon and sea trout	Failure; Level 1 not reached. Reintroduction is threatened due to climate change and warming water temperature	Migration of Rhine salmon reduces above 23°C, projections prognose up to 100 days per year of exceeding this temperature	0	1
Brunsdon <i>et al.</i> (2017)	Stocking	Releases of hatchery fish yielding density-dependent mortality	Experimental comparison of growth between two stocking practices-releasing fish in groups or dispersing them along the river	Failure; no clear benefits of spreading out releases of hatchery stockings	Mobility in fish that were clump-stocked was greater than expected	0	1
Carr <i>et al.</i> (2004)	Stocking	Decline in abundance of wild salmon	Releasing captive reared adult salmon to spawn	Failure; Level 1 not reached. Method not effective, released adults did not move upwards to spawning sites	Very few salmon fry were found the next year and these did not seem to be offspring of the released salmons	0	1
Donadi <i>et al.</i> (2019)	Habitat and water quality	Loss of exogenous shelter from wood affecting production of Atlantic salmon in rivers	Addition of large woody debris in river	Failure; no correlation between salmon abundance and woody debris in >3000 streams in Sweden	Stream width most important driver for salmon abundance	0	1
Dymond <i>et al.</i> (2019)	Stocking	Extinction of Lake Ontario Atlantic salmon in 1800s	Release of hatchery-reared salmon	Failure; small increase in salmon returns supported by hatchery. Level 1 not reached	Failure to reestablish self-sustaining salmon population from hatchery releases	0	1
Glover <i>et al.</i> (2018)	Stocking	Conservation stocking ongoing in Gironck Burn, Scotland to compensate for poor production	Conservation stocking	Failure; no overall benefit of stocking	Long time monitoring was used for the comparison of natural population regulation and stocking management and showed that conservation stocking was not effective	0	1
Horreo <i>et al.</i> (2011a)	Habitat and water quality	Decline in abundance of salmon	Foreign stocking, supportive breeding, and restoration of habitat connectivity	Failure; Level 1 not reached. Habitat restoration was promising, but supportive breeding and foreign stocking had null or negative impacts on the population	High abundance increase after barrier removal, lower than 10% abundance increase due to supportive breeding, and adverse effects of foreign stocking on local adaptability	0	1
Koed <i>et al.</i> (2006)	Habitat and water quality	Channelization, degraded habitats, forming of lake caused by subsiding soils	Restoration project with removal of dykes and meandering of river, monitoring the mortality of smolt before and after project	Failure; level 1 not reached. Naturalization of the river doubled the smolt mortality owing to bird predation. An example of unintended consequences.	Newly formed lake was prime habitat for piscivorous cormorants to settle	0	1
Koljonen <i>et al.</i> (2013)	Habitat and water quality	Channelization limiting salmon habitat resulting in low abundance	In-stream restoration project to increase available fish habitat	Failure; Level 1 not reached. Juvenile habitat improved but no response of age-one salmon	Wintertime discharge was limiting habitat availability	0	1
Larocque <i>et al.</i> (2020)	Stocking	Extinction of Lake Ontario Atlantic salmon in 1800s	Compare wild and hatchery smolt survival	Failure; wild smolts were 13.9 times more likely to survive the migration	Mortality for hatchery reared smolt was highest at release site and indicated high pre-migration mortality and stocking related mortality	0	1
Prignon <i>et al.</i> (1999)	Stocking	Extinction of Atlantic salmon due to pollution, weirs, and overexploitation	Rearing, stocking, migration study and establishing improvement proposals	Failure; Level 1 not reached. Good adaptation of stocked parr in river Ourthe basin, most smolts migrating at age two, hydropower plants cause mortality	Efficiency of stocking: minimum of 2% for eggs, 3.0% for parr, and 19.0% for pre-smolts; new fish passes are required	0	1

Table 2. Continued

Article	Category	Problem	Intervention	Result	Explanation	Success	Populations (N)
Rivinoja <i>et al.</i> (2001)	Fish passage/hydropower/stocking	Baltic salmon rivers (in this case River Umeälven in northern Sweden) have lost their natural juvenile production due to human activities blocking or reducing access to their spawning grounds, e.g. damming, power generation, and partial hindering	Construction of fish ladders in existing dams and weirs. Stocking with hatchery salmon to reduce population losses.	Failure; wild and hatchery salmon monitored through radio telemetry. Only 26% of the wild salmon and none of the hatchery salmon found the fish ladder	Salmon followed the main water discharge from the power station outlet and are thus directed away from the entrance to the bypass channel leading to the fish ladder	0	1
Saltveit <i>et al.</i> (2006)	Stocking	Stocking is undertaken in the River SuldalslÅygen, western Norway, to compensate for an estimated annual loss of 20000 Atlantic salmon smolts, <i>Salmo salar</i> L., caused by regulating the river for hydropower production	Between 160000 and 250000 one summer old fish were experimentally stocked in the study area	Failure; Level 1 not reached. Only between 6 and 10 (<0.005%) were recaptured as adults in the river. Recaptured stocked fish never exceeded 0.03% by number, despite smolts dominating the stocking material in recent years	The lack of positive response to stocking is possibly due to lesser age, smaller size and later migration of hatchery smolts, and that seawater tolerance of hatchery smolts is poorly developed, all factors increasing mortality at sea	0	1
Wallace and Curry (2017)	Stocking	Decreasing wild production in Miramichi River, Canada	Enhancement stocking of 0 + fry	Failure; Level 1 not reached. No overall benefit of stocking on site density of parr	Parr densities were lower than predicted (relative to wild parr) at sites previously stocked. Did not account for the population-level effect of brood stock removal	0	1

Papers were graded based on the levels of success that we derived, from Level 1 to Level 3, or failure (0). Uncertainties are left blank. Cases are sorted from Level 3 to Level 1, uncertainties, and then failures, with first author alphabetical organization within success categories.

(2014) reported recolonization of upstream reaches by hatchery reared salmon following reconnection of the Adour River, France.

### Success

Success was elusive in the literature, but we identified several key examples. From the review, seven salmon populations achieved a self-sustaining population (Level 1). Typically, these efforts evaluated success based on juvenile densities surveyed around the treated areas and it was not known whether the action directly enhanced progress towards biological reference points at the population scale. Four studies were successful based on improvements to habitat and connectivity. Marttila *et al.* (2019) added instream structures and reconnected spawning channels in 28 Finnish rivers, de Jong *et al.* (1997) added boulders, logs, and V-dams to Newfoundland rivers, and Calles and Greenberg (2005) built nature-like bypass channels for salmon to pass barriers in Sweden. Additionally, Hogg *et al.* (2015) confirmed that dam removal in a Maine tributary contributed to improved fish abundance by comparing to a reference site not affected by dam removal. When habitat is limiting and resulting in extreme juvenile density dependent mortality, providing access to additional habitat therefore has potential to enhance production.

The case of *G. salaris* emergency measures in Norway has been successful so far at achieving Level 1 success (Sandodden *et al.*, 2018). Complete removal of the spawning stock to eliminate the parasite from the river, followed by restocking the population using a gene bank (Table 1) implemented prior to treatment that preserved the native genetic diversity, has so far been successful, and

may soon achieve Level 3 success once stocking is ceased. Some successes reported stocking of fish, but in conjunction with other restoration efforts that addressed problems, such as Koed *et al.* (2020) where integrated efforts were made to improve habitat in Denmark and Perrier *et al.* (2014) where connectivity with upstream reaches was reestablished in the French river Adour, allowing the cultivated salmon to access previously unavailable habitat to increase production. Romakkaniemi *et al.* (2003) also suggested that rebounding of Finnish salmon populations, partly addressed by stocking rivers, coincided with a dramatic decline in marine fishing mortality in the Baltic Sea, which catalyzed stronger spawning stocks and a restoration success.

Among nine salmon populations where harvestable populations were restored (Level 3 success), eight did so by addressing habitat quality issues. Water quality issues that can be identified and remediated, for example, point source pollution, revealed good potential for recovery when spawning habitat and sufficient river connectivity were available but not fully used because of poor recruitment linked to pollution. Champion (2003) presented the case of the Tyne River in England, which is now among the best salmon producing river in the country following improvement of water quality (we note that there is debate about the role of hatcheries in restoring the river as well). Similarly, Hesthagen *et al.* (2011) presented the case for liming acidified rivers to restore water quality, resulting in Level 3 success for 13 Norwegian rivers where fisheries are now active and able to draw from the harvestable surplus. Direct improvements to spawning habitat by addition of gravel were highly successful (Barlaup *et al.*, 2008; Pulg *et al.*, 2021), as were instream enhancements to create shelter for juveniles (MacInnis *et al.*, 2008; Floyd *et al.*, 2009), including de Jong and Cowx (2016) where benefits persisted for at least 20 years following addition of boulders and V-dams in

Newfoundland, Canada. In a highly integrated effort, Koed *et al.* (2020) removed weirs and barriers, enhanced spawning grounds, and regulated fisheries in Denmark and achieved sustained Level 3 success, an example of an approach when the exact stressor could not be isolated resulted in implementation of a thorough suite of interventions implemented simultaneously.

### Failure

Many studies failed to demonstrate a consistent response to restoration measures in salmon populations. At times, this was an artifact of sampling design and not necessarily an indication that the approach was ill-conceived or unlikely to succeed. Some studies had limited follow-up intervals after intervention, making it difficult to evaluate success. There were also studies that described changes to habitat quality but not in salmon populations, making it impossible to evaluate whether a biological response occurred following intervention (e.g. Collins *et al.*, 2010). Alternatively, measurements can be made at too narrow a spatial or temporal scope for an evaluation to be made about success. Local enhancements to pools may increase local fry densities soon after intervention but be ineffective at a larger reach or along a longer timescale at actually enhancing the population. We categorized failures into two bins, for which examples are discussed below: (1) the problem was not addressed; and (2) the intervention had unintended consequences.

#### *The problem was not addressed*

In some cases, key drivers of mortality have been identified but interventions do not address them because they are too large in scale or due to a political decision. Climate change is affecting every Atlantic salmon population, especially at the southern range edge, but emissions are not being curbed enough to abate warming and the impacts on salmon populations (Jonsson and Jonsson, 2009; Todd *et al.*, 2011). More proximately, hydropower structures in rivers markedly affect salmon movement, survival, growth, and demography and their impacts are not always directly addressed in restoration efforts (Rivinoja *et al.*, 2001; McCarthy *et al.*, 2009; Izzo *et al.*, 2016). Mitigations, such as fish passage, to damming can partly be considered restoration, but have provided variable results. Rivinoja *et al.* (2001) observed only 26% of wild Baltic salmon, and no hatchery salmon, using a newly installed fish ladder in Sweden. Lundqvist *et al.* (2008) observed a similar lack of success, with an inefficient fish ladder passing only about 30% of potential spawners upstream across years up a Swedish river. Downstream migration facilities often lack completely and many downstream migration smolt and kelts are killed in hydroplants (Fjeldstad *et al.*, 2018).

Restoration efforts may also fail when the causes of a decline are misidentified, and interventions do not address the right problem. Though over €600 million were spent in the Rhine drainage to improve habitat conditions, especially connectivity (IKSR, 2020), the ecological capability of the Rhine system to support salmon still remains poor throughout the species' original range in the river. In this case, the loss of habitat and sediment quality due to hydromorphological alternations were not addressed sufficiently. In Newfoundland, Cote *et al.* (2021) found that illegal fishing was actually a driving force limiting recovery of the population in the Northwest River and community engagement helped curb illegal fishing and contributed to restoration. In Sweden, gaining trust

from river landowners was critical for gaining access to the river and having acceptance from over 4000 rightsholders (Hellström *et al.*, 2019). Poor marine survival of salmon can operate similarly; spawning habitat, juvenile shelter, and smolt abundance can be increased by restoration but to no avail for returning spawners if marine mortality is not addressed (Nicola *et al.*, 2018); this problem exists for many North American rivers where freshwater restoration is insufficient to achieve a Level III success. In Norway, sea survival is reduced by high sea lice infestations driven by intensive open net pen aquaculture, this is considered one of the main threats for the country's salmon populations (Forseth *et al.*, 2017).

#### *Unintended consequence*

Efforts to restore salmon populations are often met by unintended consequences that undermine conservation efforts. Reconnecting rivers with fishways around dams can be successful but even slight imperfections in design can be damaging. Fish ladders that have poor attractive flows or are difficult to navigate can delay or stop migration, favour certain phenotypes (e.g. small fish; Sigourney *et al.*, 2015; Maynard *et al.*, 2017), or enhance exposure to predators (Boulêtreau *et al.*, 2018). Removal of natural barriers by adding ladders around natural waterfalls or breaking beaver dams may also favour certain phenotypes or facilitate upstream penetration of escaped farmed salmon (Johnsen *et al.*, 1998). Restoration has also enhanced predation of some populations. Natural restoration of a Danish river created perfect habitat for the recolonization of cormorants and increasing predation pressure on Atlantic salmon smolts that may have offset the benefits of restoration afforded to the salmon (Koed *et al.*, 2006; Pedersen *et al.*, 2007). Restoration efforts may also enhance habitat for invasive species that negatively impact Atlantic salmon populations (Korsu *et al.*, 2010). Control or removal of predators may have similar counterproductive effects. Predators often select slow, weak, or sick prey such that predation is compensatory and not additive. Predator suppression may not affect survival where mortality is compensatory and, in some cases, may allow disease to spread, in instances where predation of diseased animals is more frequent (e.g. sockeye salmon *Oncorhynchus nerka* smolts; Miller *et al.*, 2014; Furey *et al.*, 2021).

Stocking fish reared in hatcheries is frequently reverted to as a solution to compensate for uncertainty and buy time for more decisive action to address the causes of population declines. Unfortunately, stocking is the solution most wrought with failure. Studies revealed that stocking eroded genetic diversity in a major Spanish river (Ayllon *et al.*, 2006) and selected for mismatched phenology (Bailey *et al.*, 2010). Recent studies show that hatchery fish lose their fitness in natural systems across just a few generations, which results in a strain of salmon that is less fit in wild rivers and that can outbreed with the natural populations (Fleming *et al.*, 1997; McGinnity *et al.*, 2009; Hagen *et al.*, 2019). Horreo *et al.* (2011b) observed null or negative impacts of stocking a Spanish river, which was attributed to importing foreign salmon causing introgression and loss of local adaptation (see also, Almodóvar *et al.*, 2020). An extensive evaluation of genetic effects from stocking at five sites revealed a strong reduction of effective population size (Ryman-Laikre effect) in three out of five stocked populations of Atlantic salmon in Norway (Hagen *et al.*, 2020). Hagen *et al.* (2019) additionally showed that stocking in restoration programmes may facilitate introgression of farmed genes into wild populations.

## When should hatchery stocking be applied?

Although documentation of potential negative effects of stocking are well known (Myers *et al.*, 2004), whether situations exist in which the use of hatcheries is the only viable option has not been established. Stocking has been successful at restoring populations when initial threats are addressed. For example, in Finland where stocking may have played a role in kick-starting population recovery combined with reductions in fishing mortality and other enhancements, while maintaining measures of genetic diversity (Miettinen *et al.*, 2021). In the following text, we therefore outline our perspectives on when to use hatchery stocking as an emergency measure specifically for restoring (i.e. not enhancing) salmon populations.

Despite being widely used, hatcheries can only possibly address a few salmon conservation problems when the scarcity of wild breeders is driving depensation. Why, then, do hatcheries remain such a common approach to addressing salmon restoration troubles? Young (2017) outlined seven reasons (called the “seven Hs”) why stocking persists despite overwhelming evidence against the practice. Many rivers have a **habit** of stocking, local communities get a **high** from working with fish, there is **hubris** believing that humans can improve on natural processes, and there are **honour** and **h-index** rewards for researchers that are involved in hatchery work. There is also **hope** that this may resolve troubling problems and an overall hesitance to accept the science (**heresy**). Per our definitions of success, stocking must end in order for at least Level 1 to be attained in a restoration programme and the population should then not decline when stocking ends. Yet, hatcheries are actually more likely to do harm than good for a population owing to domestication selection, which causes a loss of fitness for fish released to the wild (McGinnity *et al.*, 2009; Bolstad *et al.*, 2017). Stocked rivers consistently undergo a reduction in effective population size (Ryman-Laikre effect; Ryman and Laikre, 1991; Hagen *et al.*, 2020) due to stocking of a large number of offspring produced from a small number of broodfish (Christie *et al.*, 2012; Hagen *et al.*, 2020). Young (2017) suggested that in populations where there are enough wild spawners to support removal of broodstock for hatcheries, that population is probably not close enough to the conservation limit (Table 2; Figure 4) to justify a hatchery, but perhaps a gene bank should be made available in case of further declines and emergency measures are deemed appropriate.

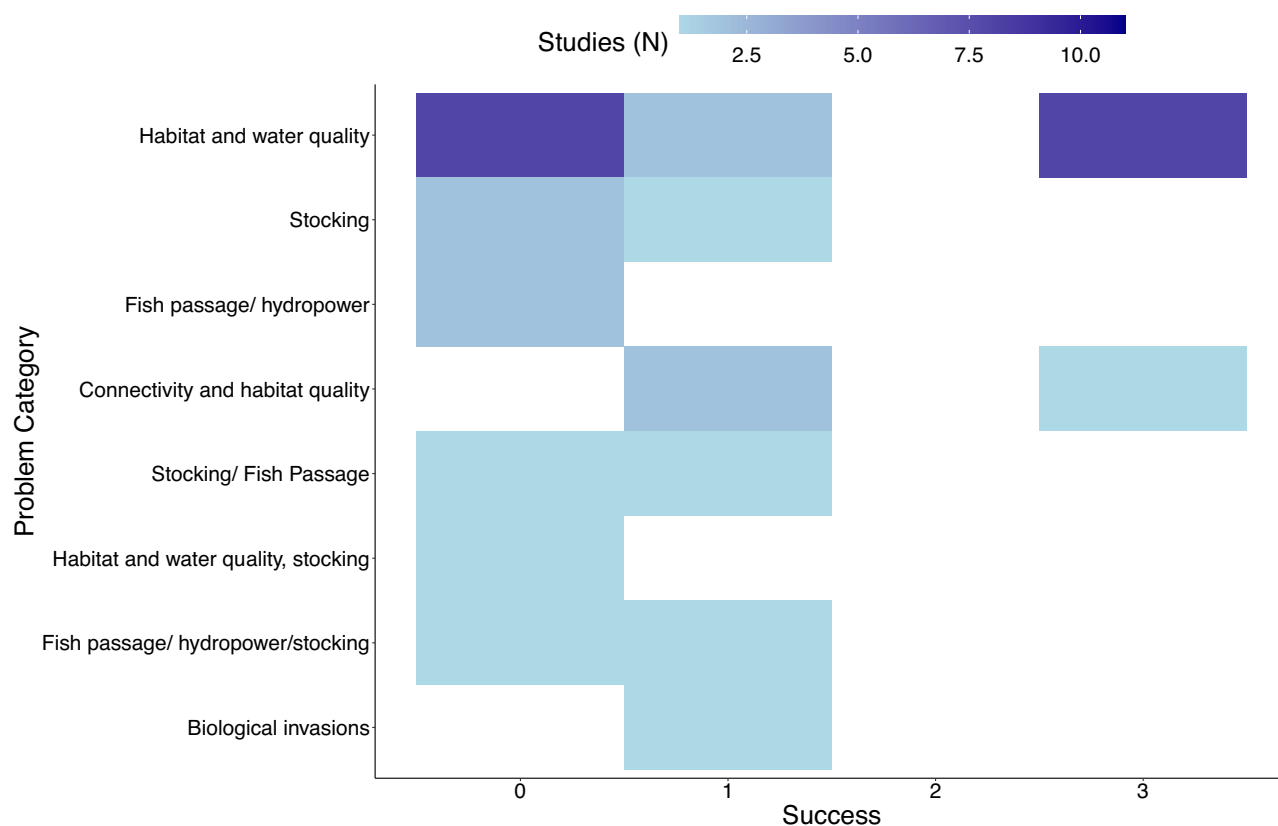
## Recommendations

The following are our collective recommendations for consideration when considering the use of hatcheries as part of restoration programmes (Figure 4):

- Thorough analyses of the extinction probability of a population should be conducted to decide whether hatchery supplementation is needed to preserve the genetic integrity and genetic variation of the population (Figure 2).
- Hatchery intervention should only be employed (1) in cases when wild populations are Endangered and when threats cannot be removed in the foreseeable future or (2) when reintroducing an extirpated population.
- Biological reference points should be established based on historical baselines and present environmental conditions, along with intermediate objectives and timelines for moving the present population back to that reference point.
- Hatcheries should be operated in conjunction with investment in efforts to address threat or threats responsible for the population's decline.
- Alternatives to hatcheries should be considered, which might have similar demographic effects without altering genetic integrity. For example, capturing and moving fry around the river to reduce density-dependent thinning (Young, 2017) or facilitated kelt reconditioning to improve overwinter survival and repeat spawning rates could be studied as possible alternatives.
- If stocking of hatchery fish is initiated, efforts must mitigate the risks of an overrepresentation of a small number of parents in the F1 generation leading to a reduction of the total effective population size in the subsequent generation (Ryman and Laikre, 1991). Ryman-Laikre effects can be addressed by finding the correct relationship between the effective number of hatchery broodfish, the proportion of stocked fish in the population, and the effective number of natural breeders (Hagen *et al.*, 2020).
- The smallest possible ratio between the number of broodfish and the effective number of broodfish should be sought, i.e. make the highest effective number of broodfish from the available broodfish. Optimization of the effective number of broodfish starts with an equal number of males and females, by producing an equal number of offspring from each broodfish, and by ensuring the hatchery produced fish are released in a manner that provides each family with an equal opportunity to survive until the act of natural selection.
- Hatchery mortality should be minimized to avoid any selective effects.
- Rearing in a protected artificial environment postpones natural selection until fish are released in the natural environment and this may lead to genetic differences between the natural and the hatchery raised fish. Given the lack of natural selection in the hatchery, hatchery residence should be as short a period as possible, meaning stocking as eggs or fry rather than as parr or smolts when feasible.
- Work with locals in a conservation framework is key to help catalyze a shift away from hatcheries while maintaining the local engagement and passion for rivers and the salmon populations that motivates many hatcheries to persist.

## Critical considerations for gene banks

- The gene bank (Table 1) should preserve the genetic integrity and as much of the genetic variation of the population as possible.
- Broodfish should be collected from a variety of phenotypes, including fish of different sizes and ages, and at different time periods in the spawning run-year, and over many years. With molecular genetic markers, stray fish from foreign populations and in particular salmon of escaped farmed origin, should be excluded. Broodfish should be selected using analyses of relatedness and a low-kinship criterion to obtain as many unrelated individuals as possible and to avoid crossings of closely related fish.
- The gene bank should be supplemented with cryopreserved milt.
- Complete and accurate records of the pedigree in the gene bank should be established, and preferably secured in more than one location.



**Figure 3.** Conceptual diagram of restoration for Atlantic salmon (*Salmo salar*). The figure provides a guide towards achieving success in restoration. As managers approach small populations with poor status (e.g. Threatened, Endangered, Critically Endangered, and Extinct), restoration is needed to work towards a self-sustaining population. A usable surplus, defined as a population size with more individuals than are needed to replace the population (i.e. beyond spawning target or carrying capacity), can provide provisioning ecosystem services in the form of valuable fisheries. Numbers correspond to levels of success.

- Strict control of diseases should occur by implementing biosafety measures that minimize the risk of introduction, establishment, and transmission of disease between wild and captive populations. All broodstock fish must be screened for diseases and the only external materials that should be introduced to the hatchery should be disinfected eggs to minimize any possible transfer of pathogens.
- For biosecurity reasons, where possible, “duplicates” of the offspring of families produced for restoration purposes should be kept at separate sites.
- If the gene bank will need to operate over multiple generations, the mating and stocking plans that are developed need to be designed to ensure that as much as possible of the genetic variation is being maintained and used.
- The survival of stocked fish from the gene bank should be monitored at different life stages (parr, smolt, returning adult, repeat spawner) and stocking plans adjusted to ensure an appropriate representation of the different families from the gene bank in the developing wild population.

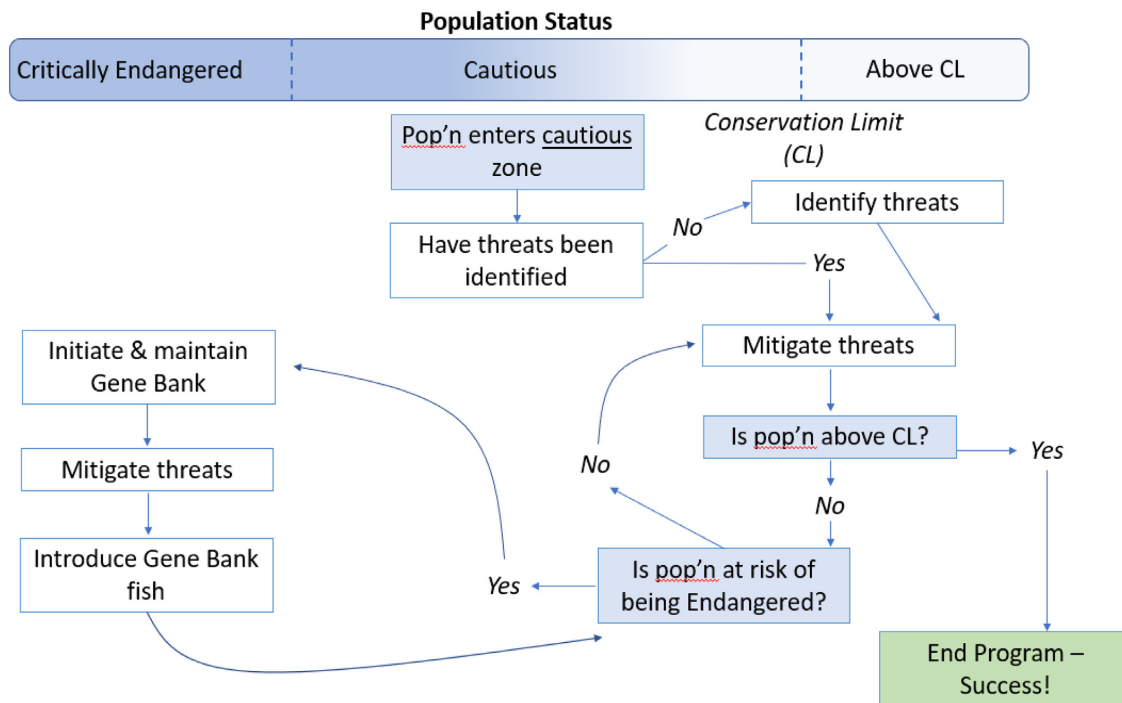
#### When the hatchery production is not stopped

Sometimes populations cannot recover beyond Critically Endangered levels despite the best attempts to address the threats (e.g. all spawning habitats has been eliminated due to the construction of

a hydropower facility and it is not possible to construct artificial spawning sites). In these scenarios, the endpoint for terminating the hatchery production is unclear and may be governed by legal constraints, political considerations, genetic objectives, social pressures, etc. In such cases, the population has not been restored, but rather is a progressively domesticated population and should be managed as such when considering the conservation status of the species in the region.

#### Are local efforts enough?

Population sizes of salmon on both sides of the Atlantic have declined since the 1980s, not only because of human impacts in rivers and coastal areas, but in many areas also because of ecosystem effects on marine mortality (Otero *et al.*, 2011; Forseth *et al.*, 2017; ICES, 2017b). Broad-scale changes in marine ecosystems are considered prominent contributors to the recent increases in marine mortality. Climate-driven changes in marine ecosystems may play a part, and region-specific hypotheses are beginning to be developed describing the causal mechanisms of the increased marine mortality experienced by stocks on both sides of the Atlantic Ocean (Todd *et al.*, 2011; Beaugrand and Reid, 2012; Chaput, 2012; Mills *et al.*, 2013; Beaugrand *et al.*, 2014; Renkawitz *et al.*, 2015; Jonsson *et al.*, 2016). Management actions to directly counteract declines due to climate and ecosystem changes in the ocean are presently not resolved be-



**Figure 4.** A schematic diagram of considerations as to when and if, when, and how to use hatcheries for conservation. Critically endangered populations may be defined differently depending on jurisdiction, but in general should be relative to biological reference points defined for a population relative to conservation limits (CR; i.e. extinction risk). CL = critical limit.

cause we know little about where salmon are exactly and what stressors they may even be encountering at a given time. However, mortality at sea seems to be density-independent for Atlantic salmon (Jonsson *et al.*, 1998). Furthermore, there are no recognized compensatory mechanisms for additional mortality at the smolt stage (Milner *et al.*, 2003; Einum and Nislow, 2011). Hence, in a situation with a reduced oceanic survival, it is even more important to ensure the sufficient number of smolts migrating to the ocean and that their condition is maximized, emphasizing the importance of freshwater restoration efforts (Thorstad *et al.*, 2021).

Another overarching impact on salmon populations is climate change. Climate change is expected to modify thermal and hydrological regimes of rivers, adding an indiscriminate challenge to restoration efforts in terms of salmon thermal performance (Karcher *et al.*, 2021), behaviour (Baisez *et al.*, 2011; Frechette *et al.*, 2018), and life history (Lennox *et al.*, 2018). Climate models have predicted a warming of air temperature and a decrease in summer precipitation in extensive portions of the wild Atlantic salmon's range (Schneider *et al.*, 2013). Given future climate change scenarios, more extreme weather (higher frequencies of violent storms, or conversely extended droughts) may severely alter natural patterns of river flow in the entire distributional range of Atlantic salmon. In Europe, strong impacts on river flow regimes are expected in the boreal climate zone over the distribution range of Atlantic salmon (Schneider *et al.*, 2013). Impacted rivers, especially smaller ones, will likely undergo extinctions of local populations when waters become too warm. By combining biological, hydrological, and hydraulic models, Sundt-Hansen *et al.* (2018) simulated how future climate change would impact the River Mandalselva in southern Norway, where discharge during summer was predicted to decline and result in reduced Atlantic salmon abundance. They found that

the wetted areas will be strongly reduced during the summer and projected increased density-dependent juvenile mortality and reductions in river carrying capacity, leading to low parr abundances and reduced abundance of smolts that would ultimately shift the spawning targets (Sundt-Hansen *et al.*, 2018). Low river flows, predicted to increase in frequency with climate change, have been shown to reduce smolt migration success in rivers with instream barriers such as weirs (Gauld *et al.*, 2013). Climate change is expected to be accompanied by a loss in biodiversity as rare or specialized species become extinct and new competitors or invasive species begin to dominate (Schneider *et al.*, 2013). River restoration efforts must be mindful of the future needs of local populations as the climate changes; Beechie *et al.* (2013) suggested that many local restoration efforts focus on small scale rehabilitation but that a focus on connectivity and flow regimes is needed to ensure efforts prepare populations for long-term changes of warming and hydrological variability.

## Conclusions and maxims

When a specific stressor is identified, when political desire to resolve it exists, and where a nucleus of the original population's genetic structure remains intact, successful restoration of Atlantic salmon populations is feasible. Successful restoration of self-sustaining populations (Level 1) and populations with harvestable surplus (Level 3) have been documented and attained. However, many failures have also occurred, especially where multiple stressors have been severe, catastrophic impacts have occurred, or efforts have relied heavily on hatchery production. Broad-scale stressors such as climate change and marine dynamics may be especially challenging to resolve. This paper was written to promote

the work that has been accomplished towards the restoration of Atlantic salmon populations and synthesize how we believe these experiences can be used effectively to support future efforts by management agencies to restore populations. In many areas, we now know enough to implement effective and evidence-based restoration efforts for salmon. Further research should be focused alongside efforts by managers and politicians to restore populations to test whether plans are working using appropriate controlled comparisons, advance new strategies such as alternatives to hatchery production, and develop evidence-based assessments of success that build on our framework and on the following maxims upon which we conclude:

1. **Avoid the need for restoration in the first place. Preserve wild stocks and manage them well.** Restoration of degraded populations is difficult and very expensive and will often fail. It is becoming harder with increasing pressure on this species especially as the climate changes and marine survival becomes more stochastic. It is incredibly challenging to restore extirpated wild populations and restoration should be prevented as much as possible. Prevention is preferred by proactively providing protection to pristine populations as much as possible (Roni *et al.*, 2002).
2. **Restoration efforts need to be relevant to resource users.** Scientific evaluation and monitoring of restoration actions should take place in collaboration with knowledge users. Depending on the jurisdiction, resource users may be Indigenous nations that are rightsholders on rivers, key land claim holders, and decision-makers; public servants (i.e. managers) that make financial allocations to restoration projects based on knowledge; or local communities where rivers form an essential part of the landscape, aesthetic, recreation, and society. Involving river users has been promising to gain acceptance and catalyze positive outcomes from restoration and is a vital part of the process (Hellström *et al.*, 2019; Cote *et al.*, 2021). Conservation human behaviour research is needed to understand how to better involve and empower river users.
3. **If the goal is for a population to be restored, we first need to identify the problems, and then take action to solve them.** Beechie *et al.* (2010) emphasize that restoration actions must resolve problems in order to be successful. Identifying the problems is often challenging, but it is apparent from the literature that when problems are identified and resolved, salmon populations can respond well, and sometimes fast. The resolution of freshwater acidification in Norway by liming rivers is a very clear example of this (Hesthagen *et al.*, 2011), as are habitat measures when, for example, spawning gravel availability limits production (Barlaup *et al.*, 2008). Salmon are good colonizers and do not necessarily need help from hatchery sources to re-establish populations if there are sources of wild genetically similar populations nearby, albeit at the expense of local genetic specialization (Perrier *et al.*, 2009). We reiterate the importance of preserving salmon populations' genetic structure, but also emphasize that genetic variability is important to protect in populations as they continue to evolve traits to adapt to a changing hydrosphere. Hatcheries are largely unnecessary and can be hindrances given the plethora of genetic problems that may arise from them (Hagen *et al.*, 2020). Hatcheries should only be used as a last resort to forestall extinction and where efforts are being made to identify and resolve stressors that are affecting the production of the population. All hatchery activities should be of the gene bank type with a focus of preserving the genetic variation and integrity be-

fore it is lost. Traditional ecological knowledge can be a valuable resource for identifying the causes of key problems and working towards resolutions with a collaborative approach that considers the role of multiple knowledge systems in restoration.

4. **Success is often possible.** Challenging problems have been resolved to restore Atlantic salmon and we can continue to overcome them with appropriate investments into research, intervention, and monitoring (especially follow-up). Roni *et al.* (2008) emphasized that brief monitoring intervals after restoration generally challenges strong conclusions about restoration success. In Norway, the parasite *G. salaris* has been eradicated from more than 40 salmon rivers that were otherwise doomed to extinction by taking swift, albeit expensive, action to preserve the genetic integrity of the population, eradicate the parasite, and restock the population from the native gene pool. Some populations in rivers that are too heavily degraded may not be salvageable, but many Atlantic salmon populations are within the capacity of managers and river stakeholders to restore with appropriate resources to identify and address underlying causes of mortality.
5. **Mysteries remain to be solved.** Although we know a lot about Atlantic salmon, perhaps more than almost any other fish species, there are still mysteries remaining to be resolved about the species and its habitat. Often, we are working to restore populations at exceptional speed compared to the natural processes that support recolonization and evolution required of stocks that have gone through genetic changes due to bottlenecks (e.g. depensation and introgression). Patience and a dedication to evidence-based implementation, scientific evaluation of success, sharing lessons of success and failure, and supporting adaptive approaches to salmon restoration are necessary to maintain a long-term vision of restoration for this iconic fish species.

## Data availability

Data are available at Zenodo.org for the regional assessments.

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## Appendix A: Geographical context of salmon restoration pressures

Please grade the following pressures, with regard to the need to solve them in order to restore populations of wild Atlantic salmon in your country

(PLEASE NOTE, EVEN IF YOU AWARE OF SOME REGIONALITY FOR A PRESSURE IN YOUR COUNTRY, STILL SCORE THE PRESSURE AS A SINGLE VALUE FOR THE WHOLE COUNTRY)

Please score each stressor as 0, no impact; 1, minor impact; 2 moderate impact; 3 major impact -use only integers, give your best estimate FOR EVERY PRESSURE LISTED!

The order of listing of stressors does NOT imply any importance of one over another

Pressure	Score
Acidification	
Migration and dispersal barriers (dams etc)	
Impacts of hydropower other than barriers (hydropowering, thermal effects, hydropower-related abstraction and habitat alteration)	
Other water abstraction (non-hydropower)	
Overexploitation by fisheries	
Channelisation, dredging (including gravel extraction) and flood control	
Sewage and organic pollution from urban sources	
Excessive nutrients and/or fine sediment from poor land management	
Hazardous chemical substances (heavy metals, pesticides etc)	
Excessive predator stress due to human influence (e.g. cormorant, seal, sawbill duck, stocked trout)	
Farmed salmon escapes	
Salmon pathogens/parasites facilitated by human action (e.g. viruses, bacteria, flukes, salmon lice)	
Invasive species	
Climate change	
Stocking of <i>S. salar</i>	
Other (please list: )	