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Research Article

Balancing the restoration of a native fish and the risks of hitchhiking invasive species

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Abstract

Reintroducing a species to an area where it is locally extinct may contribute to reestablishing the ecosystem. However, we show that such reintroductions can pose a risk to biodiversity by introducing hitchhiking invasive organisms together with the donor population. This risk was caused by more severe impacts of invasive organisms in the habitat of the donor population than the receiving environment. The freshwater resident Atlantic salmon (*Salmo salar*) in Sweden's River Klarälven perform feeding migrations to Lake Vänern. The upper part of the watershed, in Norway, lost its salmon population due to hydropower development that obstructed upstream migration. We conducted a risk assessment of the potential impacts on native ecosystems from invasive organisms associated with reintroducing Atlantic salmon into the Norwegian part of the watershed by importing adult salmon spawners. This assessment is crucial due to differences in the development of invasive organisms in the Swedish and Norwegian parts of the watershed. The risk of impacts was evaluated for invasive species, parasites, bacterial pathogens, and viruses that are present or likely present in the lower part of the watershed, or at risk of being introduced. We found a high risk of negative impacts associated with the parasite *Gyrodactylus salaris*, viral hemorrhagic septicemia virus (VHSV), *Aphanomyces astaci* causing crayfish plague, *Renibacterium salmoninarum* causing bacterial kidney disease, and *Tetracapsuloides bryosalmonae* causing proliferative kidney disease. In addition, 20 invasive species and pathogens were associated with a medium risk and three with a low risk. The case study contributes to a deeper understanding of how reestablishing locally extinct or diminished species can influence biodiversity conservation efforts and the health of aquatic ecosystems, underlining the importance of comprehensive planning in restoration projects. We highlight the importance of risk assessment of invasive species when considering the reintroduction of native species or dam removal.

Key words: environmental risk assessment, non-native species, species reintroduction, pathogens, landlocked Atlantic salmon, biological conservation, dam removal

Introduction

Freshwaters provide both habitats for a multitude of organisms and ecosystem services that are vital for human society (Vörösmarty et al. 2010). At the same time, freshwaters are largely impacted by human disturbances and may be among the most endangered ecosystems on Earth (Dudgeon et al. 2006; Kristensen et al. 2010). Worldwide, rivers are increasingly impacted by hydropower production, transport, flood protection, water diversion, agriculture, pollution, climate change, invasive species, diseases, and other habitat alterations. These factors have now caused the biological diversity of European rivers to reach a critical point (Haase et al. 2023), highlighting the need for mitigation measures to reduce adverse effects and restore healthy ecosystems.

Important mitigation measures include restoring river habitats by reintroducing native species or by removing migration barriers, such as dams. Dams alter the hydrological regime and block the free passage of migratory species in rivers and have emerged as one of the most common and severe impacts in rivers worldwide. The removal of dams or the construction of fish passage structures are emerging as effective approaches for restoring rivers and promoting environmental conservation (Ding et al. 2018; Schiermeier 2018; Silva et al. 2018). However, opening free passage for native species can potentially have detrimental consequences if it causes a spread of invasive species and pathogens. This is because invasive species are recognized as one of the major threats to biodiversity in freshwater ecosystems (Dudgeon et al. 2006; Vilizzi et al. 2021).

Atlantic salmon (*Salmo salar* Linnaeus, 1758) serves as an example of a species largely impacted by migration barriers, which cause population declines (Lennox et al. 2021). Atlantic salmon are native to the temperate and subarctic regions of the North Atlantic Ocean. The species can take on a large variety of life trajectories, but most forms are anadromous, consisting of a juvenile phase in freshwater, followed by a long ocean migration for feeding and growth, and a return migration to freshwater to spawn (Thorstad et al. 2010). Some Atlantic salmon populations are landlocked and use freshwater habitats only, but few such populations are known in Europe (Hutchings et al. 2019). Eight lakes with non-anadromous (also termed potamodromous) populations utilizing river-lake systems are known in Russia, one in Sweden (Vänern), one in Norway (Byglandsfjorden), and one in Finland (Saimaa) (Hutchings et al. 2019). Many landlocked populations have declined due to anthropogenic environmental impacts, and some populations have become extinct (Hutchings et al. 2019; Ozerov et al. 2010). The greatest threats to the persistence of landlocked salmon in Europe are habitat degradation and development for hydropower production (Hutchings et al. 2019). Freshwater populations often show a particularly high degree of local adaptations through natural selection and genetic divergence compared to other anadromous Atlantic salmon populations

(Bourret et al. 2013), highlighting the need to conserve the unique landlocked salmon populations.

In Lake Vänern (hereafter Vänern), Sweden, landlocked Atlantic salmon populations were isolated for thousands of years due to isostatic rebound following deglaciation, which cut the lake off from the sea (Nilsson et al. 2001). Adult salmon from one of the populations migrate from Vänern to the River Klarälven (hereafter Klarälven) to spawn. After hatching, juveniles reside in the river for two to three years before migrating back to Vänern for feeding. The River Trysilelva (hereafter Trysilelva), and associated tributaries or rivers and lakes in Norway, constitutes the upper parts of the Klarälven watershed. Landlocked Atlantic salmon from Vänern could reach the upper parts of the Klarälven watershed before hydropower plants were built from 1904 to 1961, but are now extinct in the upper parts of the watershed. The Atlantic salmon population in the Klarälven watershed has declined by 95% due to overfishing, dam construction, hydropower development, timber floating, and industry (Hedenskog et al. 2015; Olstad et al. 2020). Approximately 88% of the watershed stretches inhabitable for Atlantic salmon are in Norway (Thorstad et al. 2021), yet the population is now confined to the lower Klarälven section in Sweden.

Species reintroduction is often an attractive method in conservation work (Ripple and Beschta 2012; Seddon et al. 2007) and is defined as "the intentional movement and release of an organism inside its indigenous range from which it has disappeared" (IUCN/SSC 2013: p. 3). The local Norwegian authorities have proposed to reintroduce Atlantic salmon to Trysilelva through importation of adult salmon spawners. These fish, captured in the lower parts of Klarälven in Sweden, would be transported in tanks, and released in the Norwegian part of the watershed to spawn. After some years, the juveniles would migrate back to Vänern as smolt. Hence, reintroducing adult salmon spawners in tanks is not a permanent solution since the adult fish need to be moved annually. Due to the obstruction over recent decades of free fish migration through the river system, there has been a divergence in the occurrence of invasive species and pathogens between the Swedish and Norwegian parts of the watershed. Man-made connections between Vänern and other watersheds facilitate a potential spread of invasive species and pathogens to Vänern. In addition, four timber flumes connect Trysilelva to River Glomma (hereafter Glomma), the largest watershed in Norway, which may facilitate the spread of invasive species and pathogens to a larger area. If these invasive species and pathogens were to become introduced, spread and established in Norway, they could potentially have significant ecological impacts. Such risks need to be carefully considered prior to the implementation of any reestablishment efforts (McLaughlin et al. 2013).

Here, we assess potential negative effects on biodiversity and ecosystems associated with reintroduction of this native but locally extinct Atlantic

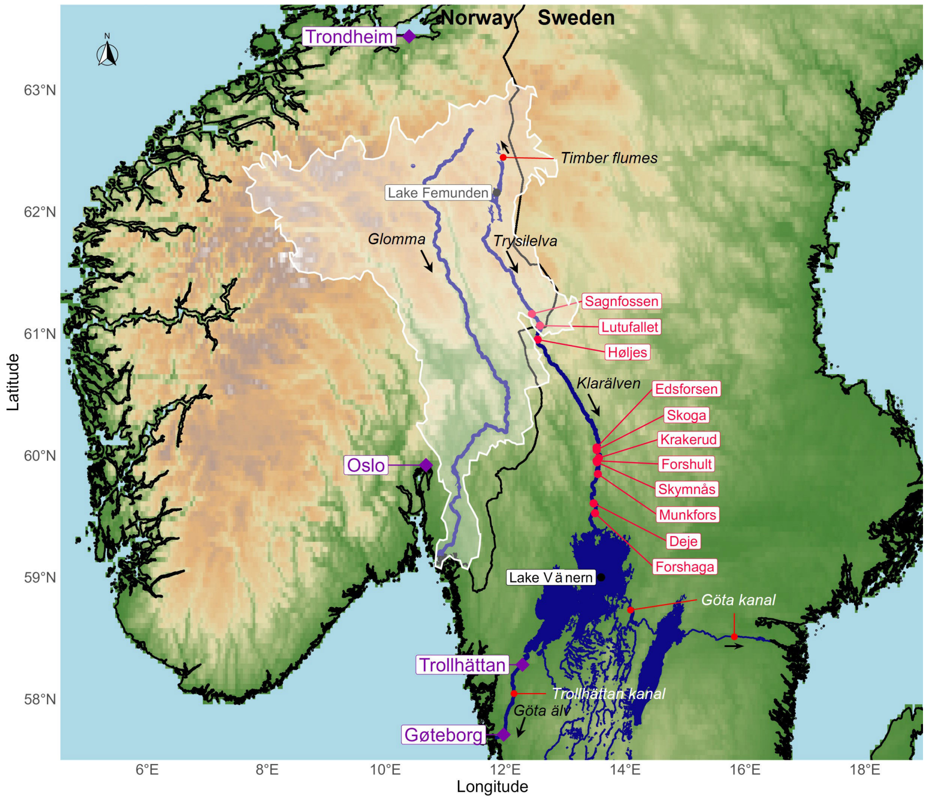

Figure 1. Map of Trysilelva and Klarälven from Femunden to Vänern, including the Göta kanal and Trollhätte kanal, and the timber flumes that connect the Klarälven watershed to the Glomma watershed. The power plants are indicated in red on the map, while the white area represents the combined Glomma and Trysilelva watersheds in Norway. The arrows indicate the direction of water flow.

salmon to Trysilelva. We present an environmental risk assessment that includes invasive species and pathogenic infective organisms. To the best of our knowledge, this is the first time such a comprehensive risk assessment has been performed prior to the re-introduction of a native species. The example we present may be representative of many cases where specimens are moved between sites or migration barriers are removed, thus allowing free passage of migrating species. We address the broader implications of such reintroductions, including the balance between conserving native species and managing the risks associated with invasive species and pathogens.

Materials and methods

Study area

Vänern and Trysilelva/Klarälven are part of the longest watershed in Scandinavia, shared between Norway and Sweden (Hedenskog et al. 2015) (Figure 1). The watershed originates in Lake Rogen in Sweden and continues into Norway to Lake Femunden, (hereafter Femunden) and thereafter through several smaller lakes and rivers to Trysilelva. Trysilelva flows back into Sweden, where it changes its name to Klarälven. Klarälven enters Vänern, which is the largest lake in Sweden and the third largest lake in Europe. Vänern drains into the Kattegat Sea area through the River Göta älv, entering the sea at Gothenburg on the Swedish west coast. The elevation difference between Femunden and Vänern is 617 meters, and the length of the Trysilelva/Klarälven river course is about 400 km (Hedenskog et al. 2015).

The Klarälven catchment is significantly affected by the generation of hydropower, with eleven hydroelectric plants constructed from the early 20th century up until the 1960s. Nine of these plants are in Klarälven, while the remaining two are in Trysilelva (Figure 1). Höljes Power Plant is the largest facility and the only one with an upstream reservoir, whereas the remaining power plants are run-of-the-river facilities (Hedenskog et al. 2015). All power plants include dams that block upstream fish migration, except the two uppermost power plants in Trysilelva where fish passages are installed (Hedenskog et al. 2015). When the Höljes power plant was built in the 1960s, this ended the migration of Atlantic salmon and brown trout (*S. trutta* Linnaeus, 1758) to upstream areas, including Trysilelva and all stretches that used to be accessible to migrating salmonids in the upper watershed (Hedenskog et al. 2015).

Some notable man-made waterways connect the Klarälven watershed to other watersheds. The Trollhätte kanal (82 km) and the Göta kanal (191 km) form parts of a 390 km long waterway, creating a navigable path from Gøteborg on the west coast to the Baltic Sea. Opened in 1800 and 1832, respectively, the Trollhätte kanal and the Göta kanal facilitated the introduction of migrating species into Vänern from the Kattegat and the Baltic Sea. Consequently, Vänern today hosts numerous non-native species (Josefsson and Andersson 2002). The Glomma watershed in Norway, which includes the country's longest river, Glomma, has a catchment area of 47,400 km^2, while the Norwegian part of the Klarälven watershed covers 5,400 km^2 (source: https://nevina.nve.no/). There are no natural connections between the two watersheds. However, a canal featuring four timber flumes was constructed in 1715 between Femunden and Lake Feragen, linking these two watersheds. This canal was used for timber transport until 1973 and was restored in the 1990s. Since 2010, it has been included in a UNESCO World Heritage Site. Several species have spread from Femunden to the Glomma watershed after the timber flumes were constructed, such as northern pike (*Esox Lucius* Linnaeus, 1758), European perch (*Perca fluviatilis* Linnaeus, 1758), European whitefish (*Coregonus lavaretus* (Linnaeus, 1758)), grayling (*Thymallus thymallus* (Linnaeus, 1758)), burbot (*Lota lota* (Linnaeus, 1758)), and common minnow (*Phoxinus phoxinus* (Linnaeus, 1758)). Invasive organisms hitchhiking with reintroduced Atlantic salmon could spread along the same pathway and reach a large area of Norway.

Risk assessment

The risk assessment was based on a literature review and qualitative evaluation by expert judgement. The risk of impacts on native biodiversity and ecosystems

Table 1. Ratings used to assess the magnitude of the negative impact.

Rating	Descriptors
Minimal	No known impact on native biodiversity and ecosystems
Minor	Potential impact on biodiversity and ecosystems, but only occasional deaths of individuals, hence minor effect on biodiversity and ecosystems
Moderate	Impact may cause a moderate reduction in viability and adaptability of native populations, hence moderate impacts on biodiversity and ecosystems
Major	Impact may cause severe reductions in native populations, hence major impacts on biodiversity and ecosystems
Massive	Impact may cause severe reductions in native biodiversity (local extinctions), hence massive impacts on biodiversity and ecosystems

Table 2. Ratings used to assess the likelihood of the negative impact.

Rating	Descriptors
Very unlikely	Negative consequences would be expected to occur with a likelihood of 0-5%
Unlikely	Negative consequences would be expected to occur with a likelihood of >5-10%
Moderately likely	Negative consequences would be expected to occur with a likelihood of >10-50%
Likely	Negative consequences would be expected to occur with a likelihood of >50-75%
Very likely	Negative consequences would be expected to occur with a likelihood of >75-100%

Table 3. Ratings used for describing the level of confidence for both impact and likelihood.

Rating	Descriptors
Very low	There is very little or no published data on the topic. Only expert judgment used
Low	Available information on the topic is limited, and we use mostly expert judgments
Medium	Some published information exists on the topic, but expert judgments are still used
High	There is sufficient published information, and expert judgments are in concurrence
Very high	The topic is very well debated in peer-reviewed journals and international reports. Expert judgments are in concurrence

was assessed for relevant free living invasive species and pathogenic infective organisms (bacteria, viruses, and parasites). We first identified invasive species and pathogenic infective organisms that may spread to the upper Klarälven watershed with reintroduction of Atlantic salmon. For each of the invasive species and pathogens, we then assessed the magnitude of the potential negative impact on native biodiversity and ecosystems if they become established (Table 1), and the likelihood that the negative impact would occur (Table 2). The likelihood of impact includes a combined assessment of the likelihood: 1) that the invasive species and pathogens will be transferred to Norway with the fish transports, and 2) that the invasive species and pathogens will have a negative impact if introduced. Likelihoods are expressed as percentages to reduce ambiguity and increase consistency across different assessments (Burgman 2005). The level of confidence for both magnitude and likelihood was also included, based on available data (Table 3). The conclusion of the assessments in terms of low, moderate, or high risk, was based on the product of the magnitude and likelihood for the impact in question. All categories were thoroughly discussed among the experts prior to performing the risk assessment to ensure a common understanding.

Results

We identified various organisms that might spread to the upper Klarälven watershed. These species are currently found in Sweden but not beyond the

Höljes power plant in Trysilelva in Norway. The organisms also include those that are currently absent but have active pathways for entering Vänern, Klarälven, and its tributaries, making their introduction likely. The organisms were categorized into four groups: invasive species, viral pathogens, bacterial pathogens, and pathogen parasites. First, we present the specific organisms. Then, we assess their potential magnitude of impact on biodiversity in Norway, and the likelihood that an introduction and establishment will occur via the transport of Atlantic salmon into Norway.

Invasive species

The signal crayfish (*Pacifastacus leniusculus* (Dana, 1852)) was introduced from North America to Europe in the 1960s. This species is known to adversely affect aquatic ecosystems, such as stream invertebrates, freshwater pearl mussel (*Margarita margaritifera* (Linnaeus, 1758)), noble crayfish (*Astacus astacus* (Linneaus 1758)), salamanders, and salmonids, and can carry the oomycete pathogen *Aphanomyces astaci* Schikora, 1906 (Skurdal et al. 2017; Velle et al. 2021). A notable behavior of the signal crayfish is its tendency to create burrows, which can become dense (up to 14 per square meter) and cause the collapse of riverbanks. The dispersal of signal crayfish is often due to deliberate and unlawful introductions for culinary purposes, and accidentally through activities such as fish relocation or via contaminated fishing nets and boats. The signal crayfish is established in around 5000 locations in Sweden, including the Vänern watershed (Bohman and Edsman 2011). In Norway, it has been detected in ten sites between 2006 and 2021 (Velle et al. 2021). Overall, the signal crayfish will have a moderate impact (high confidence). This is unlikely to occur (low confidence).

The Chinese mitten crab (*Eriocheir sinensis* H. Milne Edwards, 1853) is an invasive species in North America and Europe (Herborg et al. 2007; Veilleux and Lafontaine 2007). It poses serious ecological and economic threats and can also carry the oomycete pathogen *A. astaci* (Svoboda et al. 2017). It has been sporadically found in Norway, including in the Glomma estuary (Krog et al. 2009). Its ability to complete its life cycle in Norway remains uncertain. In Sweden, consistent sightings of this crab along coastal areas date back to the 1930s, and it is now prevalent in Vänern (Drotz et al. 2010; Drotz et al. 2012). The crab’s small larval stages are easily transported in water, but mature crabs must migrate to estuaries for spawning. The nearest estuary to the Trysilelva region is about 300 kilometers away, reachable through a series of rivers, timber flumes, and lakes. Overall, the Chinese mitten crab will have a major impact (high confidence). This is very unlikely to occur (medium confidence).

The round goby (*Neogobius melanostomus* (Pallas, 1814)) is a euryhaline and bottom-dwelling fish from central Eurasia. It is invasive and has considerable ecological and economic effects (Corkum et al. 2004). This species outcompetes many native species, rapidly dominating resources, such as food, hiding spots, and nesting sites (Poos et al. 2010). Additionally, it preys effectively on various organisms (Fitzsimons et al. 2009). In the Gulf of Gdańsk, the round goby's parasite fauna includes at least 12 species (Kvach and Skóra 2007), and it hosts the invasive and parasitic nematode *Anguillicoloides crassus* (Kuwahara, Niimi & Itagaki, 1974) in the Baltic Sea (Kvach 2004). Round goby has established large populations in the Baltic Sea and along the Swedish west coast at the mouth of the River Göta älv (Puntila et al. 2018). However, it has not been detected in Vänern. The round goby lays its eggs on hard surfaces like stones, shells, and aquatic plants, which suggests that egg introduction via water is unlikely. Overall, the round goby will have a major impact (medium confidence). This is very unlikely to occur (medium confidence).

The zebra mussel (*Dreissena polymorpha* (Pallas, 1771)) is a small freshwater bivalve. It is one of the most aggressive invasive species in freshwater environments globally (Karatayev and Burlakova 2022). Its invasive success is attributed to its broad ecological niche, and rapid population growth. As an ecosystem engineer, it alters and creates new habitats, influencing trophic dynamics and food availability for both pelagic- and benthic species (Karatayev et al. 2002; Strayer 2009) and has detrimental impacts on ecology, economy, and ecosystem services (McKindsey et al. 2007; Strayer 2009). It competes with the native freshwater pearl mussel (Ricciardi et al. 1998). Zebra mussels inhabit lakes in Sweden but have not been found in Vänern (von Proschwitz and Wengström 2021). They require ion-rich water to proliferate, particularly magnesium (Hallstan et al. 2010). A natural barrier of soft-water lakes separates the zebra mussel populations in eastern Sweden from Vänern. Overall, the zebra mussel will have a massive impact (high confidence). This is very unlikely to occur (medium confidence).

The Canadian pondweed (*Elodea canadensis* Michaux, 1803) is an aquatic plant native to North America. It forms dense mats that disrupt human activities, hinder water flow, block sunlight, create anoxic conditions, and accumulate sediments, adversely affecting water quality, habitats, and ecosystems (Barrat-Segretain 2005; Josefsson and Andersson 2002; Simpson 1984). Such changes can alter native plant community compositions (Mjelde et al. 2012) and cause crayfish population declines (Hessen et al. 2004). The species has spread across Europe (Josefsson 2011), driven by broad ecological adaptability, asexual reproduction, rapid regeneration from small fragments (Redekop et al. 2016), and dispersal of fragments via water, waterfowl, and humans (Anderson et al. 2014; Spicer and Catling 1988). Canadian pondweed was introduced to Norway in the 1920s and was found in 101 locations by 2013 (Anglès d'Auriac et al. 2019). In Sweden, it is widespread, including around Vänern (Palmgren 2005). Overall, Canadian pondweed will have a major impact (high confidence). This is unlikely to occur (medium confidence).

Viral pathogens

The infectious haematopoietic necrosis virus (IHNV) is the causative agent of infectious hematopoietic necrosis (IHN), a disease resulting in high mortality among various fish species, including Atlantic salmon (Dixon et al. 2016; St-Hilaire et al. 2002). Juvenile fish are particularly susceptible, and those that survive an infection become lifelong carriers. While IHNV is not found in Vänern today, the ongoing importation of susceptible species poses a risk for introducing the virus. This includes the importation of European eel (*Anguilla anguilla* (Linnaeus, 1758)) into Vänern and its catchments, and rainbow trout (*Oncorhynchus mykiss* (Walbaum, 1792) that are used in aquaculture and put and take fisheries. After introduction, there will be no effective measures to either limit the spread of IHNV or mitigate its impact. In 2022, IHN was detected in Denmark for the first time after rainbow trout imports from Germany (Sommerset et al. 2022; Vendramin et al. 2021). Before the detection was made, however, the virus had spread further to eight farms and three put and take lakes in Denmark, and also to Åland in Finland by export of rainbow trout (Sommerset et al. 2022). Overall, IHNV will have a major impact (medium confidence). This is moderately likely to occur (low confidence).

The viral haemorrhagic septicemia virus (VHSV) has caused significant mortality in various fish species in the Great Lakes region of the United States and Canada. It causes high mortality, can infect over 80 fish species and has a notable capacity for adapting to new hosts (Bootland and Leong 1999; OIE 2019). In 2019, VHSV outbreaks occurred in Austria, Belgium, the Czech Republic, France, Germany, Italy, Poland, and Switzerland (EURL 2019). Currently, VHSV is not found in Vänern. However, the importation of susceptible species, such as rainbow trout for aquaculture and put-and-take fisheries, poses a risk for introducing VHSV to Vänern, Klarälven, and their tributaries. Should VHSV be introduced into Trysilelva, its further spread via fish migration in connected water bodies is likely. Presently, there are no effective measures to limit the spread of VHSV or reduce its impact on affected fish populations. Overall, VHSV will have a massive impact (very high confidence). This is moderately likely to occur (low confidence).

There are many genetically distinct strains of the piscine orthoreovirus (PRV). PRV-1 causes heart and skeletal muscle inflammation (HSMI) in Atlantic salmon (Palacios et al. 2010; Wessel et al. 2017), and can also infect other salmonids (Di Cicco et al. 2018; Purcell et al. 2020). PRV-2 causes Erythrocytic Inclusion Body Syndrome in coho salmon (*O. kisutch* (Walbaum, 1792)) (Takano et al. 2016). PRV-3 causes a disease resembling HSMI in rainbow trout (Olsen et al. 2015) and is also a prevalent virus in wild anadromous brown trout (Garseth et al. 2019). In this context, PRV-1 is the most relevant genotype. HSMI, caused by PRV-1, is characterized by abnormal swimming behavior, anorexia, and mortality rates of up to 20% (Kongtorp et al. 2006). PRV-1 is prevalent in farmed Atlantic salmon

(Sommerset et al. 2022) and has been found in wild Atlantic salmon and anadromous brown trout in Norway and other countries (Garseth and Biering 2018; Madhun et al. 2018). In Sweden, a study of wild Atlantic salmon revealed PRV-1 in one of 24 tested fish in River Mörrum on the south coast (Vendramin et al. 2019). The status of PRV-1 in the Vänern water course remains unknown. Seventy-two percent of rainbow trout farms were found infected with PRV-3 in Denmark (Sørensen et al. 2020), suggesting PRV-3 may also be present in farmed rainbow trout in Vänern. Introduction of PRV-3 will have a moderate impact (medium confidence), and is unlikely to occur (medium confidence). Introduction of PRV-1 will have a minor impact (low confidence), and is moderately likely to occur (medium confidence).

Aquabirnaviruses, found in aquatic environments globally, infect a wide range of aquatic organisms including numerous fish species, mollusks, and crustaceans (Gamil et al. 2015). Among these, the infectious pancreatic necrosis virus (IPNV) is known for causing acute catarrhal enteritis in salmonids (Rodriguez Saint-Jean et al. 2003). IPNV is particularly harmful to juvenile salmonids and can be transmitted via roe. Mortality rates during outbreaks range from very low to 90%, and surviving fish often become lifelong carriers. IPNV is notable for its resistance to disinfectants and its ability to remain infectious over extended periods in both seawater and freshwater. In Norway, the virus is predominantly found in farmed Atlantic salmon during both their freshwater and marine phases, leading to approximately 20 outbreaks annually (Sommerset et al. 2022). In Sweden, IPNV is present in coastal areas and was detected in Vänern in 2016 (Axén et al. 2020). Overall, IPNV will have a minor impact (medium confidence). This is moderately likely to occur (medium confidence).

The salmon gill poxvirus (SGPV) is a member of the Orthopoxviridae family and is the causative agent of salmon gill poxvirus disease affecting farmed Atlantic salmon (Gjessing et al. 2015). This virus is prevalent among both farmed and wild Atlantic salmon populations, though it has not been found in other species of fish. Symptoms in afflicted salmon include breathing difficulties, diminished appetite, and a susceptibility to additional infections. SGPV has been recorded in aquaculture along the coast of Norway and in Canada, the Faroe Islands, Iceland, and the UK (LeBlanc et al. 2019; Sommerset et al. 2022). However, SGPV occurrences have not been reported in landlocked salmon in Norway. SGPV has not been found in the export or import areas in the Vänern watershed. Overall, SGPV will have a minimal impact (low confidence). This is unlikely to occur (medium confidence).

Fish rhabdoviruses (other than VHSV and IHNV) belong to the Sprivivirus, Novirhabdovirus, and Perhabdovirus (Hoffmann et al. 2005; Stone et al. 2013). These viruses have been identified in many wild and farmed fish species in marine and freshwater environments and cause significant mortalities (e.g., Björklund et al. 1994; Dannevig et al. 2001; De Kinkelin et al. 1973).

Examples include grass carp rhabdovirus, tench rhabdovirus, pike fry rhabdovirus, *Siniperca chuatsi* rhabdovirus, eel rhabdovirus European X, eel virus American, perch rhabdovirus, Swedish sea trout virus, European lake trout rhabdovirus, snakehead rhabdovirus, hirame rhabdovirus, and eelpout rhabdovirus. The presence of rhabdoviruses in the Vänern watershed is unclear due to the lack of monitoring. However, it is believed that rhabdoviruses will emerge in Europe in the coming decades. Given their capacity for host-switching, these viruses are expected to affect a variety of fish hosts (Pallandre et al. 2021). Overall, rhabdoviruses will have a moderate impact (very low confidence). This is moderately likely to occur (low confidence).

The infectious salmon anaemia virus (ISAV) belongs to the Orthomyxoviridae family and includes the non-virulent ISA-HPR0 and the virulent ISA-HPRdel. Whereas ISA-HPR0 causes a transient infection of epithelial cells of gills and the skin, ISA-HPRdel infects and propagates in endothelial cells, causing serious disease and mortality (Evensen et al. 1991; Mjaaland et al. 2002). The HPR0 viruses have widespread distribution in the fresh- and saltwater phases of both farmed and wild salmon populations. Most countries farming Atlantic salmon have experienced outbreaks, but the virus has not been reported in Sweden. ISAV can be carried by multiple fish species, including wild Atlantic salmon, brown trout, and rainbow trout. The susceptibility of northern pike, European perch, European whitefish, Arctic char (*Salvelinus alpinus* (Linnaeus, 1758)), and grayling is unknown. Overall, ISA-HPR0 will have a minimal impact (medium confidence). This is moderately likely to occur (low confidence). ISA-HPRdel will have a moderate impact (low confidence). This is moderately likely to occur (low confidence).

The salmonid alpha virus (SAV) is a virus belonging to the Togaviridae family. Depending on strain and fish species, it causes pancreatic disease or sleeping disease in salmonid fishes in both fresh- and saltwater fish (Deperasińska et al. 2018). Infected fish display reduced appetite, circulatory disturbance, and loss of exocrine pancreatic tissue in the late phase (Jansen et al. 2017). Six genotypes have been classified based on sequence data (SAV1-6), where SAV2 occurs in both freshwater and seawater. SAV infections have been documented from most places where Atlantic salmon or rainbow trout are farmed in Europe (Sommerset et al. 2022). The documented host range for SAV includes Arctic char, Atlantic salmon, common dab (*Limanda limanda* (Linnaeus, 1758)), and rainbow trout at all life stages. Most natural infections occur in seawater, but may likely occur during the freshwater parr stage of Atlantic salmon (McVicar 1990). SAV has not been documented in Vänern. Overall, SAV will have a moderate impact (low confidence). This is moderately likely to occur (low confidence).

Bacterial pathogens

Renibacterium salmoninarum Sanders and Fryer, 1980 causes the severe condition bacterial kidney disease (BKD) in salmonids. The bacterium can transmit vertically (Evelyn et al. 1985) and fish can become lifelong subclinical carriers (Jónsdóttir et al. 1998), making eradication difficult. The infection status in Femunden and Trysilelva watershed remains unknown, but it has not been detected in landlocked Atlantic salmon or brown trout in Norway (Garseth et al. 2020). In Sweden, *R. salmoninarum* was first reported in 1985 and has since spread inland and along the coast. BKD outbreaks were recorded in rainbow trout in the Vänern watershed in the late 1980s and early 1990s. The occurrence of minor, undetected BKD outbreaks among wild salmonid populations remains a possibility. In 2019, BKD was diagnosed in farmed fish at six locations in Sweden and in a wild Arctic char in Lake Vättern (Axén et al. 2020). Overall, *R. salmoninarum* will have a major impact (medium confidence). This is likely to occur (low confidence).

Aeromonas salmonicida subsp. *salmonicida* Austin et al., 1989 causes the severe disease furunculosis (or "classical" furunculosis) primarily in salmonids (Cipriano and Bullock 2001). Prior to vaccination in Norwegian salmon aquaculture in the early 1990s, the disease spread to several Norwegian rivers, where it caused significant mortalities in wild salmon and trout (Johnsen and Jensen 1994). A few waterways along Norway's west coast remain endemically infected (Garseth et al. 2022; Sommerset et al. 2022). The bacterium has never been detected in Trysilelva, and the current infection status in the upper Klarälven watersheds is unknown. Furunculosis has been reported in Swedish salmonid aquaculture, including four cases in 2019, none of which were connected to Vänern (Garseth et al. 2020). A diverse range of so-called "atypical" *A. salmonicida* variants, associated with a similarly diverse range of clinical manifestations collectively termed "atypical" furunculosis in fish, also exists (Gulla et al. 2019). This bacterial group has a worldwide distribution, with the multitude of variants often showing affinity for a narrow range of host species, where they may cause serious disease. At least five variants have been documented from Sweden (Gulla et al. 2019), including at least one in a river draining into Vänern (Garseth et al. 2020). Overall, *A. salmonicida* subsp. *salmonicida* will have a major impact (medium confidence). This is moderately likely to occur (low confidence). "Atypical" furunculosis will have a minor impact (low confidence). This is moderately likely to occur (low confidence).

Flavobacterium psychrophilum (Bernardet and Grimont 1989 *ex* Borg 1960) Bernardet *et al.* 1996 may cause severe disease primarily in salmonid fry and parr. The bacterium is commonly found in temperate freshwater environments, and strains differ in virulence and host specificity (Nilsen et al. 2014). Some have been spread via anthropogenic activities (Nicolas et al. 2008). Vertical transmission of *F. psychrophilum* is likely possible, and its potential to reside within egg cells makes it resistant to disinfection (Brown et al. 1997; Cipriano 2005). *F. psychrophilum* is a frequent cause of disease in farmed rainbow trout in Sweden (Garseth et al. 2020). It is likely present in the Vänern watershed given its prevalence in freshwater environments. However, it remains uncertain whether strains found in these areas are capable of infecting or causing disease in Atlantic salmon. In Norway, *F. psychrophilum* is sporadically detected in salmonid species, including Atlantic salmon (Sommerset et al. 2022). Overall, disease due to *F. psychrophilum* infection will have a minor impact (medium confidence). This is moderately likely to occur (low confidence).

Flavobacterium columnare (Bernardet and Grimont 1989 *ex* Davis 1922) Bernardet *et al.* 1996 causes columnaris disease, which can lead to high mortality in wild fish populations (Declercq et al. 2013). The bacterium potentially affects a wide range of fish species. *F. columnare* typically becomes a concern at water temperatures around 18–22 °C and is rarely associated with disease below 15 °C (Austin and Austin 2012). To date, *F. columnare* has not been reported in Norway, but has been found in salmonid fish farms in Sweden (Axén et al. 2020). Given the ongoing global warming, the significance of *F. columnare* in Northern Europe may increase. Overall, the impact of *F. columnare* will be moderate (low confidence). This is unlikely to occur (low confidence).

Yersiniosis is caused by *Yersinia ruckeri* Ewing et al., 1978 and constitutes a significant disease problem in salmonid aquaculture. Although it is mainly found in farmed rainbow trout around the world, in Norway, this disease is predominantly identified in farmed Atlantic salmon (Sommerset et al. 2023). While only a small proportion among a wide range of *Y. ruckeri* genotypes/strains have been extensively linked to fish disease (Gulla et al. 2018), low-virulent strains have been shown to be widespread in freshwater environments connected to salmonid aquaculture in Norway (Riborg et al., 2022) and this may also be the case for Vänern and surrounding watersheds. Overall, the impact of *Y. ruckeri* will be minimal (medium confidence). This is moderately likely to occur (low confidence).

Parasites

Gyrodactylus salaris Malmberg, 1957 causes gyrodactylosis in Atlantic salmon. This monogenean infests the external surfaces of many salmonids, but only Atlantic salmon suffer from severe disease. In Norwegian rivers, *G. salaris* has been responsible for severe disease outbreaks in Atlantic salmon parr, with an average mortality rate of 86% (Johnsen et al. 1999, Mo 2024). While *G. salaris* is not native to Norway, it is naturally found in lakes and rivers that drain into the Baltic Sea (Kudersky et al. 2003; Kuusela et al. 2007; Malmberg and Malmberg 1993; Meinilä et al. 2004). The first detection of *G. salaris* in the Vänern watershed was in 1972 on rainbow trout at a fish farm (Malmberg and Malmberg 1993). The parasite was first observed on Atlantic salmon in Vänern in 2013 (Olstad et al. 2013). To date, three closely related haplotypes of *G. salaris* have been identified on salmon in Klarälven and Vänern (Olstad et al. 2013). Overall, *G. salaris* will have a massive impact (high confidence). This is likely to occur (medium confidence).

The parasitic ciliate *Ichthyophthirius multifiliis* Fouquet, 1876 is responsible for white spot disease, which affects many freshwater fish species, including salmonids. This disease can impact various stages of salmonids and other freshwater fish, potentially altering their behavior and making them more susceptible to predation. Disease outbreaks can occur in water temperatures as low as 6 °C but are most common during the warmest part of the year (Dickerson 2012). Such outbreaks have been observed in spawning wild salmonids (Traxler et al. 1998). More recently, outbreaks of white spot disease were reported in European eel in the river Ätran and other rivers along the Swedish west coast (C. Axén, Swedish Veterinary Agency, *pers. comm.*). Overall, *I. multifiliis* will have a moderate impact (medium confidence). This is moderately likely to occur (medium confidence).

The myxozoan parasite *Tetracapsuloides bryosalmonae* (Canning et al., 1999) causes proliferative kidney disease (PKD) in salmonids, typically manifesting when water temperatures exceed 15 °C (Okamura et al. 2011). The disease predominantly harms the kidney and spleen of salmonids and has 60 to 70% mortality rates (Sterud et al. 2007). Individuals that recover can carry *T. bryosalmonae* without showing disease symptoms (Soliman et al. 2018) and develop immunity. The life cycle of *T. bryosalmonae* involves bryozoans as the primary host and salmonids as the secondary host *Tetracapsuloides bryosalmonae* can also influence the growth and viability of its bryozoan hosts adversely (Tops et al. 2009). The parasite has been detected in Atlantic salmon, brown trout, Arctic char, and European whitefish in several rivers and lakes in Norway (Mo and Jørgensen 2017; Oredalen et al. 2022), though similar monitoring efforts in Swedish rivers are lacking. Overall, *T. bryosalmonae* will have a major impact (high confidence). This is very likely to occur (medium confidence).

The myxozoan *Myxobolus cerebralis* Hofer, 1893 causes whirling disease in salmonids (Hoffman 1990). This parasite targets the nervous system and inflicts damage to the cartilage and backbones during early life stages (Gilbert and Granath 2003). As a result, the swimming ability of the affected fish is compromised, making them more vulnerable to predation. Reports confirm the presence of *M. cerebralis* in salmonid populations in both Norway and Sweden (Alexander and Bartholomew 2020). However, the exact geographical distribution of this parasite in wild salmonids is unknown. Overall, whirling disease will have a moderate impact (low confidence). This is likely to occur (medium confidence).

Parasitic crustaceans belonging to the genus *Salmincola* are referred to as gill maggots since they attach to the gills of freshwater fish, especially salmonids, where they feed on blood and tissue. Gill maggots have typically little impact on their fish hosts, although they can have serious impact when becoming very numerous (Black 1982). Their presence can impair the respiratory efficiency of the host. This can make the fish more susceptible to predation and other adverse effects, particularly when water temperatures rise, and dissolved oxygen levels decrease (Vaughan and Coble 1975). Species of *Salmincola* are documented in salmonids in both Norway (Amundsen et al. 1997; Kusterle et al. 2012; Mo et al. 1998) and Sweden (GBIF 2023). Their presence and distribution in the Vänern watershed are unknown. Overall, gill maggots will have a minor impact (medium confidence). This is moderately likely to occur (medium confidence).

The parasitic nematode *Anguillicoloides crassus* causes inflammation and bleeding in the swim bladder of European eel (Kirk 2003). The parasite uses several hosts and trophic levels to complete its life cycle (De Charleroy et al. 1990), which may potentially impact the broader aquatic ecosystem (Sjöberg et al. 2009; Wlasow et al. 1998). *Anguillicoloides crassus* was introduced to Europe with imports of live Japanese eel (*Anguilla japonica* Temminck & Schlegel, 1846) in the 1980s. The first record of *A. crassus* in Sweden was in 1988 from coastal areas (Höglund and Andersson 1993). It was later found in Swedish lakes, most likely because of eel stocking (Wickström et al. 1998). *Anguillicoloides crassus* is not reported from Vänern. However, it may be present since European eel has repeatedly been stocked in the lake. In Norway, *A. crassus* was first observed in a fish farm (Mo and Steien 1994) and has later been observed in eel in the lower part of a few rivers (Mo 2009). Overall, *A. crassus* will have a moderate impact (low confidence). This is unlikely to occur (medium confidence).

The oomycete *Aphanomyces astaci* causes crayfish plague, which is a lethal disease in noble crayfish. This pathogen, native to North America, is asymptomatically carried by North American crayfish species. The widespread introduction of signal crayfish in Sweden has led to the decimation of 98% of all native crayfish populations from 1900 to 2020 (Bohman and Edsman 2011; Jussila and Edsman 2020). *A. astaci* can spread both through its crayfish host and independently in water. Signal crayfish is established in Vänern. Crayfish plague is less prevalent in Norway compared to Sweden, but it has eradicated several populations of noble crayfish in Norway (Vrålstad et al. 2014). Overall, crayfish plague will have a massive impact (high confidence). This is moderately likely to occur (medium confidence).

Risk characterization

The summarized risks of negative impacts on native biodiversity and ecosystems from importing adult Atlantic salmon spawners from the lower reaches of the Klarälven watershed to the upper reaches of the watershed in Trysilelva are depicted in Figure 2. There is a high risk associated with *A. astaci*, VHSV, *G. salaris*, *R. salmoninarum* and *T. bryosalmonae*. In addition, there

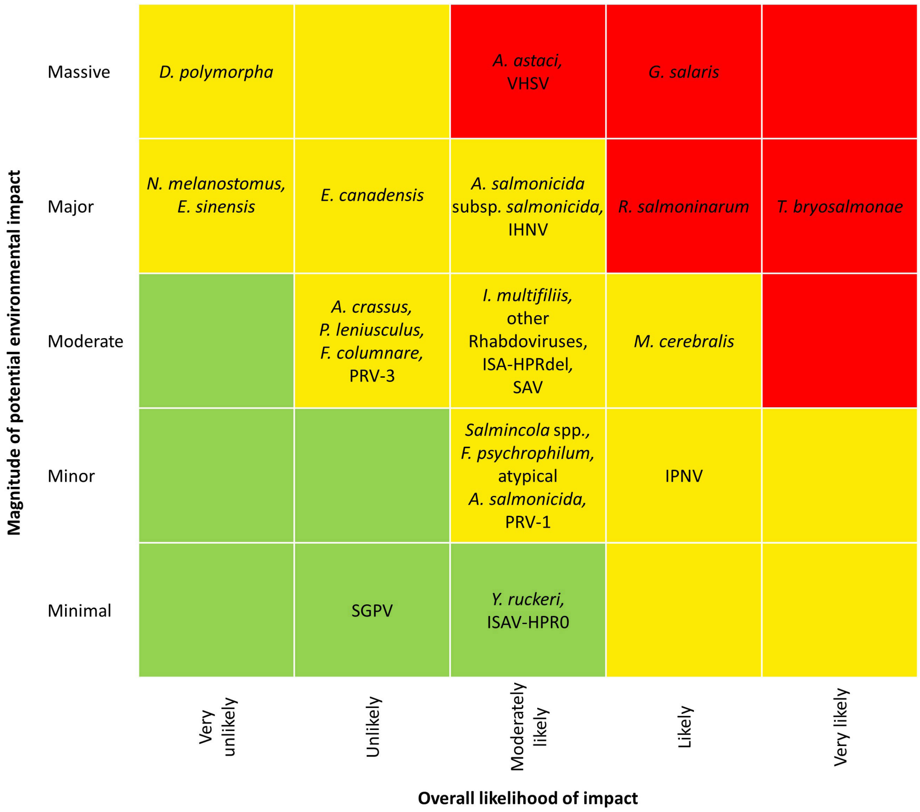

Figure 2. Risk associated with the introduction of invasive species, parasites, and viruses with the transfer and release of adult Atlantic salmon (*Salmo salar*) from Klarälven in Sweden to the upper part of the watershed in Trysilelva in Norway. Green = low risk, yellow = moderate risk, red = high risk.

is a moderate risk associated with 20 invasive species and pathogens, and a low risk associated with three pathogens.

Discussion

Sustainable ecosystem management and conservation efforts involving species reintroduction and habitat restoration should depend on knowledge-based ecological and regulatory frameworks (Velle et al. 2022). Global restoration efforts provide insights into the complexity of reintroducing species and restoring habitats. Learning from these experiences can enhance the effectiveness of future projects and reduce unintended effects. Reports of failed projects and risk assessments that led to project cancellation should also be included. These can serve as important resources for learning, helping to refine strategies and approaches in ecosystem restoration efforts. However, reports of failed projects or negative results are scarce and lack uniformity (Catalano et al. 2019; McLaughlin et al. 2013).

Although Atlantic salmon can survive spawning and spawn multiple times, the high mortality at power plants during downstream migration makes it unlikely for fish to survive for consecutive spawning seasons (Hedenskog et al. 2015). Still, our study on Atlantic salmon in the Klarälven watershed has shown that moving fish to upstream reaches may enhance the spread of invasive species and pathogens. In addition to a relatively rich native fauna and flora, Vänern hosts numerous non-native species, with intentional introductions including various fish species and the North American signal crayfish, alongside ornamental plants like Canadian pondweed (Josefsson and Andersson 2002). Unintentional introductions, such as the zebra mussel and Chinese mitten crab, likely arrived through ballast water (Josefsson and Andersson 2002). In addition, pathogens and parasites have spread from human activities, such as fish farming (Axén et al. 2020). The potentially significant ecological impacts of both intentional and accidental species introductions are well-documented (Clavero and García-Berthou 2005; Early et al. 2016).

Five of the invasive species and pathogens we assessed are associated with a high risk for biodiversity and 20 are associated with a medium risk. The invasive parasite *G. salaris* is one of the high-risk species, and previous introductions to Norway have demonstrated the destructive effects and considerable costs associated with such an invasion. *Gyrodactylus salaris* was introduced to Norway with import of infested fish and has spread via transport of infested fish between hatcheries and rivers. The parasite has had devastating effects on Atlantic salmon populations in 53 Norwegian rivers (Mo 2024). The parasite has now, as of May 2024, been eradicated from 43 Norwegian rivers where Atlantic salmon populations have also been restored at a cost of NOK 1.5 billion for research, monitoring, and eradication (Mo 2024). Indirect costs are significantly larger when considering funding for management, impacts on fish farms, and the reduction in tourism and fishing. The signal crayfish is an example of one of the medium- risk species in our assessment. This species can outcompete native species for resources and habitat, leading to declines in native biodiversity (Skurdal et al. 2017; Velle et al. 2021).

The results in our study, underscore the complex outcomes of reintroducing a locally extinct species from a source population, which in our case is analogous to an opening of migration barriers. A reintroduction of Atlantic salmon in the upper reaches of the watershed aims to boost biodiversity, ecosystem functions, and cultural use of the river, which is often the outcome when migration pathways are restored (Duda et al. 2021; Maloney et al. 2008). Yet, it can potentially disrupt ecological balances by enhancing the spread of invasive species and pathogens. Because of increased risk of invasive species causing the extinction of native species, some have argued for isolating habitats instead of enhancing connectivity (Hess 1994; Simberloff et al. 1992). In line with this, exclusion barriers, such as dams and weirs, have been used as a management strategy to control the spread of aquatic invasive species (Holthe et al. 2005; Jones et al. 2021).

Our findings are contextualized against the dam removal movement (Bellmore et al. 2017; O'Connor et al. 2015). Dam removal initiatives globally share common themes, such as concerns for public safety when the dams are old, economic reasons, and ecological restoration and reestablishment of historical migration pathways, aiming to restore water bodies to their natural state (Hart et al. 2002; O'Connor et al. 2015). For example, there are about one million dams in Europe, and the EU Biodiversity Strategy aims to restore river flow by removing unnecessary dams by 2030. The focus is often on smaller, low-barrier dams, influenced by the Water Framework Directive aiming to improve the ecological status of water bodies. However, it is necessary to carefully consider the ecological consequences of such projects. Indeed, previous studies have reported that invasive species can spread post dam removal (Freeman and Bowerman 2002; Orr and Stanley 2006; Tullos et al. 2016). In addition, dam removal may induce the spread of bioaccumulated toxins to upstream reaches through migrating fish (Freeman and Bowerman 2002). The removal of dams or the construction of fish passages, which enhances the spread of both native and invasive species (McLaughlin et al. 2013), is referred to as a "connectivity conundrum" (Zielinski et al. 2020). Our study indicates that the connectivity conundrum is also highly relevant when fish are moved between sites within a watershed with limited connectivity.

Performing risk assessments using available literature and expert judgments is common in environmental risk analysis (Burgman 2005). However, this method has potential weaknesses, such as data limitations, possible subjectivity from expert opinions, and the dynamic nature of ecosystems that a static assessment might not fully capture (Dwyer 1990; National Research Council 1994; Wilkins 2003; Burgman 2005; Landis et al. 2013). Also, trying to understand and quantify interactions with coexisting native species is complex (Harrison and Cornell 2008), making predictions regarding introduction of invasive species challenging (Jeschke et al. 2014). This task is further complicated by ongoing climate change, which is expected to exacerbate the impacts of some pathogens (Elad and Pertot 2014; Marcos-López et al. 2010) and cause species geographical range shifts (Trisos et al. 2020). Our risk assessment has concentrated on a selected group of agents with well-established pathogenic potentials, as well as other organisms that may spread with Atlantic salmon as a biological vector and/or with its transportation water as a mechanical vector. A plethora of pathogens have been documented in freshwater Atlantic salmon populations in Norway and Sweden (Bakke and Harris 1998), but our understanding regarding their overall implications and prevalence is often lacking (Josefsson and Andersson 2002; Miller et al. 2014). There is also a possible cumulative effect resulting from the accidental introduction of accompanying invasive species and pathogens (Tamburello and Litt 2023; Westby et al. 2019). Such cumulative effects are especially likely to occur in native fish, given the number of potential pathogens that can spread to fish with reintroduced Atlantic salmon.

Additionally, there is uncertainty regarding the future risk of introducing new pathogens through various means, such as aquaculture, introduction of imported European eels, put-and-take fisheries, ballast water, and other human activities. Lastly, the re-introduction of Atlantic salmon in the upper parts of the watershed will likely impact the current ecosystem. The most likely impact of reintroducing Atlantic salmon is a reduction in the brown trout population in the rivers due to competition for space and food as juveniles, and for spawning areas (Hesthagen et al. 2017). Feeding Atlantic salmon juveniles may also impact the density of benthic macroinvertebrate prey in rivers, though such effects are difficult to predict (Wooster 1994). Given uncertainties related to species interactions, climate change, lack of understanding about pathogens, potential cumulative effects, potential new pathogens, and the impact caused by Atlantic salmon, our risk assessment is likely conservative.

To reduce the risk of spreading invasive species and pathogens when reintroducing Atlantic salmon to the upper Klarälven watershed, broodfish stocks should undergo screening procedures before transfer from Sweden to Norway. However, since many infectious agents often occur at low levels or prevalence in wild fish and/or may be found only in specific organs or persist in latently infected carriers, not detecting them across a small sub-selection of samples/specimens would not guarantee their absence (Riborg et al. 2022; Suzuki et al. 2017). Moreover, stress caused by handling and moving may result in activation of sub-clinical infections with subsequent shedding and transmission to naïve fish (Riborg et al. 2022). Another precaution would be to place the broodfish in quarantine, during which they should be closely monitored for signs of disease and tested for infectious agents. Additionally, sterilizing spill water, equipment, and other materials could help eliminate invasive species and pathogens. Two more comprehensive risk mitigation strategies would be (1) to import fertilized eggs to a local Norwegian hatchery and release eggs directly into rivers or release them as juveniles or smolts, and (2) to import fertilized eggs and establish a long-term broodstock in Norway using the live gene bank approach (Bøe et al. 2021). From this broodstock, eggs can either be released into rivers or raised in a local hatchery for later release as juveniles or smolts. Both mitigation measures reduce the risk, especially the second one, as decreasing transportation water lowers impact likelihood, and transporting only eggs enhances disease control.

When it comes to future needs, a continuous and comprehensive ecological monitoring, including appropriate biodiversity metrics, is crucial for assessing the long-term impacts of species reintroduction and habitat restoration (Sinclair et al. 2024). This will help in understanding the resilience and adaptability of ecosystems to restoration efforts. The management should be targeted and adaptive, allowing for the continuous monitoring of reintroduced species and ecosystem responses. This strategy enables the adjustment of management practices based on real-time ecological feedback, emerging knowledge, and changing environmental conditions. Also, there is a need to develop more sensitive and specific disease screening technologies that can detect a wide range of pathogens in various life stages of reintroduced species. The high-throughput qPCR (HT-qPCR) approach represents an example of such technologies (Teffer et al. 2020; Teffer and Miller 2019). This allows for preemptive management actions to prevent introduction and establishment of unwanted infectious agents in restored populations. The development of ecological models that can accurately simulate the outcomes of species reintroduction and ecosystem restoration efforts would also be of great use. These models may incorporate several factors, such as bioenergetics, ecological interactions, climate change scenarios, and human impacts, to provide insights into what factors that are most important to the success of reintroductions and unintended consequences (D'Acunto et al. 2023; Halford et al. 2024). Finally, the socio-economic implications of species reintroduction and dam removal projects are multifaceted, potentially impacting local communities, economies, cultural values, and ecosystems. Future studies should aim to quantify these impacts through an interdisciplinary approach.

Conclusions

This study illustrates the dual-edged nature of species conservation exemplified by the landlocked Atlantic salmon in the upper parts of the Klarälven watershed. It aims to restore a key ecosystem component and cultural river use, but also risks spreading invasive species and pathogens, threatening native populations and ecosystems. This mirrors global instances where species reintroductions caused unforeseen ecological impacts. We recommend against reintroducing Atlantic salmon now due to significant uncertainties about the presence of pathogens. Additionally, there are substantial challenges in reestablishing the population and ensuring welfare, especially given the high mortality rates of juvenile salmon migrating downstream through power plants.

Looking ahead, reintroduced species have the potential to thrive in restored ecosystems, especially given changing climate and land-use patterns that will significantly affect species distributions and future biodiversity (Bellard et al. 2012). However, the success of reintroduction projects relies on understanding ecological dynamics, monitoring, and managing risks of introducing pathogens and invasive species. This requires a multidisciplinary approach, combining scientific research, stakeholder collaboration, and adaptive, knowledge-based management practices.

Authors' contribution

GV: original draft, sample design and methodology, investigation and data collection; data analysis and interpretation; EBT: research conceptualization, sample design and methodology, investigation and data collection; data analysis and interpretation, writing – review and editing; ÅHG: investigation and data collection; data analysis and interpretation, writing – review and editing; TG: investigation and data collection; data analysis and interpretation, writing – review and editing; SG: investigation and data collection; data analysis and interpretation, writing –

review and editing; HL: investigation and data collection; data analysis and interpretation, writing – review and editing; TAM: investigation and data collection; data analysis and interpretation, writing – review and editing; MM: research conceptualization, sample design and methodology, data analysis and interpretation, writing – review and editing.

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