



UPPSALA
UNIVERSITET

Evaluation of River Restoration Measures: Interstitial Habitat Variables and Salmon Hatching Rates as Indicators of Success

Jonas Emanuelsson

Degree project in biology, Master of science (2 years), 2023

Examensarbete i biologi 45 hp till masterexamen, 2023

Biology Education Centre, Uppsala University, and Department of Ecology and Genetics/Limnology,
and County Administrative Board of Gävleborg

Supervisors: Sebastian Sobek and Karl Gullberg

External opponent: Sarah Shakil

Table of Contents

Abstract	2
1. Introduction	3
1.1 Background.....	4
1.1.1 The riverine environment	4
1.1.2 Atlantic salmon.....	9
1.1.3 Human activities and river ecosystems	13
1.1.4 River restoration	16
1.2 Aims.....	19
2. Study area	20
2.1 Sampling sites.....	21
3. Materials and methods.....	24
3.1 Modification of Whitlock-Vibert boxes	24
3.2 Egg handling, excavation of redds and egg planting.....	25
3.3 Sampling of hyporheic water.....	26
3.4 MWVB retrieval, hatching rate and accumulation of fine sediments	27
3.5 Statistical methods	28
4. Results	29
5. Discussion	35
6. Conclusions	38
Acknowledgements.....	39
References	39
Appendices	49

Abstract

River ecosystems are some of the most complex ecosystems on Earth, characterized by a highly heterogeneous environment which is able to sustain a disproportionately high level of biodiversity in relation to the area of which they occupy. However, anthropogenic activities are encroaching on the highly diverse riverine landscape, threatening freshwater biodiversity. Species with complex life cycles involving migrations between marine and freshwater environments are disproportionately threatened. One such species is the Atlantic salmon, which now is at historically low population levels. Restoration efforts are being made to restore degraded river ecosystems and strengthen salmonid populations. However, the response from salmonids and other organisms used as indicators for restoration success are inconclusive or lacking. Additionally, evaluation of restoration success lacks standardized procedures and tools for monitoring. Habitat variables have been shown to be robust indicators when assessing restoration success. This study attempts to assess restoration success using an accessible and user-friendly tool which can be used for measurements of both biotic and abiotic variables. Salmon eggs were planted in the riverbed at potential spawning grounds, from where hyporheic water was extracted to measure physicochemical habitat variables which are critical to salmon embryos. The results indicate that the functionality of available spawning habitats in the study area is adequate in both restored and non-restored sections. Habitat variables displayed spatial variation but were not more favorable at restored sites compared to non-restored sites. Similarly, egg hatching rate varied spatially but not between restored and non-restored sites. The apparent lack of response to the restoration efforts in the study area is likely due to a combination of factors such as biased site selection, limited sampling period and a lack of comparable pre-restoration values. This highlights the need of defined restoration goals, a robust monitoring plan and criteria for evaluation of restoration success. Nevertheless, the method used in this study can be applied to measure biotic and abiotic variables and may add to the toolbox for assessing restoration success. This will hopefully contribute to new insights for monitoring and evaluation of restoration success in other projects.

1. Introduction

This master's thesis is done in cooperation with the County Administrative Board of Gävleborg (Länsstyrelsen Gävleborg) and their ongoing project "Re-introduction of wild salmon and naturally-reproducing sea trout in Dalälven" (Återintroduktion av vildlax och naturligt reproducerande havsöring i Dalälven), which is funded by Vattenfall AB, Fortum AB and The Swedish Society for Nature Conservation (Naturskyddsföreningen). The project is attempting to re-introduce salmon (*Salmo salar*) to the Gysinge and Sevedskvarn areas (henceforth Gysinge) of lower Dalälven (Nedre Dalälven). Salmon have been absent from Gysinge since the damming of the river in the early 1900's. However, future fish passages or other technical solutions may provide salmon with a migration route and a yearly production of up to 33.000 juvenile salmon in the Gysinge area (if fully restored), according to a previous survey (Hagelin *et al.* 2018). Considerable river restoration efforts were made in 2016 and 2018 to facilitate the re-introduction of salmon to the area. Additionally, using egg planting containers, 160.000 to 215.000 salmon eggs have been planted annually within the project since 2019 (L. Calamnius, unpublished observations). Electrofishing, egg hatching rate and eDNA is currently used to evaluate the progress of the project. The results indicate that egg hatching rates has been high, and salmon have been detected using eDNA methods. However, only a few juvenile salmon have been caught during yearly electrofishing surveys, indicating a low survival rate from egg to juvenile. The eggs which are planted in egg planting containers are placed directly on top of the riverbed. This means that the planted eggs are exposed to surface water flow and conditions which may differ from the hyporheic environment where wild salmon bury their eggs at a depth of 15-25 cm down into the riverbed substrate (Bardonnnet & Baglinière 2000). Since there is no salmon currently spawning in the Gysinge area, the functionality of the restored sections as potential spawning sites for a future salmon population is unknown at this stage. Ecosystem functionality can be defined as the ability of the system to sustain production, stability and other functions (Mittelbach & McGill 2019) and is rarely monitored or evaluated in restoration projects (Harrison *et al.* 2019, Pulg *et al.* 2022).

Insufficient monitoring and evaluation of success is a subject of concern in river restoration (Jähnig *et al.* 2011, Weber & Peter 2011, Morandi *et al.* 2014, Wohl *et al.* 2015, Louhi *et al.* 2016, Rubin *et al.* 2017), and standardized procedures and improved tools for monitoring and evaluation are needed (Jähnig *et al.* 2011, Morandi *et al.* 2014, Marttila *et al.* 2016, Nilsson *et al.* 2016, Louhi *et al.* 2016, Rubin *et al.* 2017, Foote *et al.* 2020). Common tools such as electrofishing are known to produce inconclusive results and is therefore not an ideal tool for monitoring of restoration success (Koljonen *et al.* 2013, Foote *et al.* 2020). Measurements of hyporheic physicochemical variables are often used to assess salmonid status (Soulsby *et al.* 2001, Youngson *et al.* 2004, Sternecker *et al.* 2013a, Saltveit & Brabrand 2013, Casas-Mulet *et al.* 2015, Sear *et al.* 2017, Lavery & Cunjak 2019, Hauer *et al.* 2020). However, only a few studies have used physicochemical variables to evaluate the ecological functionality of restored river sections (Pander *et al.* 2009, Sternecker *et al.* 2013b, Zimmer & Lautz 2015, Mrozińska *et al.* 2018). Ecological indicators are often used to evaluate restoration success. An ecological indicator must be easy to monitor, while at the same time be able to capture ecosystem complexity (Dale & Beyeler 2001, Weber & Peter 2011, Pander & Geist 2013). Preferably, instead of a single indicator species, a group of biotic and abiotic indicators should be used. For example, egg hatching rate of a target species and life stage-specific habitat variables can be monitored to evaluate if requirements of the target species are fulfilled (Pander *et al.* 2009, Pander & Geist 2013). A combination of physical and biological habitat variables has been

shown to be robust ecological indicators (Wright 2021). The development and survival of salmonid eggs and alevins (i.e. recently hatched juveniles) are highly dependent on hyporheic habitat variables (Sternecker *et al.* 2013a). Previous studies on salmonids have shown that suboptimal water quality may lead to high mortality, reduced growth and retarded development in early life stages (Luckenbach *et al.* 2001, Luckenbach *et al.* 2003). The hyporheic environment where salmon eggs are naturally deposited is structurally and functionally separated from the surface water and exhibits gradients in environmental variables (Findlay 1995) which can be monitored (Alexander & Caissie 2003, Calles *et al.* 2007, Pander *et al.* 2009, Sternecker *et al.* 2013a, Sternecker *et al.* 2013b, Lavery & Cunjak 2019).

This study will attempt to further develop methods based on Whitlock (1995) and Pander *et al.* (2009) for evaluation and monitoring of restoration success in regards of ecosystem function (functionality of spawning grounds). A combination of abiotic and biotic variables will be used to assess if restoration efforts in lower Dalälven at Gysinge have improved the conditions which are critical to early life-stages of salmon. Abiotic habitat variables were measured in the hyporheic environment of restored and non-restored river sections. The biotic variable egg hatching rate will be determined based on salmon eggs planted in the hyporheic environment of restored and non-restored river sections. Additionally, the same measurements will be made in the egg planting containers used by the County Administrative Board of Gävleborg, to assess if the conditions in the containers resembles the natural conditions of the riverbed. The methods applied in this study could help monitoring and evaluation of restoration success in other projects. The results may also provide answers for stakeholders regarding factors which could limit future salmon production in the Gysinge area.

1.1 Background

1.1.1 The riverine environment

Rivers and streams as ecosystems

The rivers and streams (hereafter used interchangeably) of the Earth forms a network of ecological systems which connects the terrestrial, freshwater and marine environments (Allan & Castillo 2007). Rivers are important drivers of biogeochemical cycles, primary transporters of nutrients to the oceans and regulators of greenhouse gases (Jacobson *et al.* 2000, Raymond *et al.* 2013). Additionally, rivers hold high cultural values (Carothers *et al.* 2021, Woollorton *et al.* 2022) and have provided humans with vital ecosystem services throughout the history of civilization (Macklin & Lewin 2015, Hanna *et al.* 2018). Malin Falkenmark, one of the first Swedish female hydrologists, once described the flow of water as “*the bloodstream of the biosphere*”, because all other biological systems depend on water for their existence (Falkenmark 2003). The large-scale variation and spatial distribution of river ecosystems are determined by the interactions of climate, topography, geology and land cover (Snelder & Biggs 2002). The highly dynamic and heterogeneous riverine environment enables river ecosystems to sustain a disproportionally high level of biodiversity, in relation to the area of which they occupy (Ward *et al.* 2002, Dudgeon *et al.* 2006). Despite only containing 0.01% of all Earth’s water and covering 0.8% of the Earth’s surface, rivers and other freshwater ecosystems house 9.5% of all known species and more fish species than the oceans (Likens 2009, Strayer & Dudgeon 2010).

Much of modern river ecology builds upon the work by Noel Hynes, a freshwater biologist who suggested that a river is a product of its surrounding environment (Hynes 1975). Hynes is likely

to have set off the wave of research which eventually culminated in different theories and conceptual models such as the *River Continuum Concept* (Vannote *et al.* 1980), *Nutrient Spiraling Theory* (Newbold *et al.* 1981), *Flood-Pulse Concept* (Junk *et al.* 1989), *Natural Flow Regime* (Poff *et al.* 1997), *Riverine Ecosystem Synthesis* (Thorp *et al.* 2006) and the *River Wave Concept* (Humphries *et al.* 2014). Recent research based on the conceptual models indicates that they are insufficient and not able to fully explain the variability of river ecosystems (Collins *et al.* 2018, Maasri *et al.* 2021). While conceptual models are helpful for testing hypotheses and understanding river ecosystems, the generality and applicability of the conceptual models can be questioned as they attempt to simplify one of the most heterogeneous, dynamic and complex ecosystems of Earth. This is something Hynes touched upon back in 1975, when he concluded that “*every stream is likely to be an individual and thus not really very easily classifiable*” (Hynes 1975). River ecosystems are structurally and functionally different from other ecosystems, because of intrinsic characteristics such as the *hierarchical structure* of drainage networks, *unidirectional flow* of water and *four-dimensional nature* (Ward 1989, Allan & Castillo 2007).

Rivers are *hierarchically structured* with microhabitats nested within larger habitats such as a riffle, which in turn is a part of a reach. A reach is then nested within a stream segment and the segment is a part of a tributary stream connected to the larger river network within a catchment (Frissell *et al.* 1986). The hierarchical and dendritic structure implies that local conditions are regionally controlled (Frissell *et al.* 1986). The position in the river is key. According to Vannote *et al.* (1980), ecological processes occur in a predictable pattern from the headwaters to the river’s mouth. The network position hypothesis states that biodiversity patterns and community assemblies are controlled by the position in the river network (Schmera *et al.* 2018).

The *unidirectional flow* of water is a master variable with ubiquitous influence on ecosystem parameters such as channel morphology, transportation of matter, nutrient cycling, mixing of the water column and life-strategies of riverine organisms (Newbold *et al.* 1981, Junk *et al.* 1989, Allan & Castillo 2007, Humphries *et al.* 2014). Flow is highly variable, which is why each river is unique and has its own flow regime that regulates the ecological processes in the river (Poff *et al.* 1997, Biggs *et al.* 2005). In a boreal river, the natural flow regime is generally defined by predictable flow peaks in spring due to the snowmelt and in the autumn following heavy precipitation, while summers and winters usually are defined by low and stable flow conditions (Arheimer & Lindström 2015).

The *four-dimensional nature* of rivers describes the *longitudinal, lateral, vertical and temporal dimensions* of rivers (Ward 1989) (Fig. 1). The *longitudinal dimension* (Fig. 1) is related to the *River Continuum Concept*, how stream position can define local ecosystem attributes (Vannote *et al.* 1980, Allan & Castillo 2007). Physical processes such as sediment flux can display longitudinal patterns (Montgomery 1999), with the river divided into source, transport and response reaches (Montgomery & Buffington 1997). While rivers are hierarchically structured, they also exhibit a patchy distribution of discrete habitats along the longitudinal profile, with varying environmental conditions that determines community compositions and ecosystem functioning on a smaller scale (Thorp *et al.* 2006). Habitat patches supports local ecological communities which are connected through interactions and the exchange of individuals and genetic material. In other words, river organisms are structured in metacommunities (Altermatt 2013, Schmera *et al.* 2018). Therefore, many of them are dependent on the longitudinal connectivity to sustain healthy populations (Winemiller *et al.* 2010, Altermatt 2013, Van Looy

et al. 2019). The *lateral dimension* (Fig. 1) describes how the riverine and terrestrial environments are connected through the exchange of energy and matter (Ward 1989, Junk *et al.* 1989, Baxter *et al.* 2005). The exchange across the river-terrestrial boundary mainly occurs in the riparian zone and floodplains (Thorpe *et al.* 2006) (Fig. 1). The riparian zone is the ecotone that connects aquatic and terrestrial environments (Fig. 1). Riparian communities often consist of both aquatic and terrestrial species, enhancing the regional biodiversity (Naiman & Décamps 1997, Décamps *et al.* 2009). Additionally, the riparian zone provides shading and buffers against pollution from sediment, organic and chemical compounds, which is retained by riparian vegetation and soil taxa (Naiman & Décamps 1997). Similarly, floodplains are hotspots for biodiversity, sediment trapping and biogeochemical cycling (Junk *et al.* 1989). Another important aspect of the lateral dimension is the inundation of floodplains (Junk *et al.* 1989). Nutrients and organic material from the river are deposited on land during inundations, thereby increasing the productivity of regularly flooded areas. As the flood recedes, organic matter produced on the floodplain is released back into the river as allochthonous input (terrestrially derived organic matter) (Junk *et al.* 1989). Allochthonous input may consist of riparian plant litter or soil organic matter and forms the base of riverine food webs together with in-situ primary production (autochthonous input) (Cummins 1974, Vannote *et al.* 1980). The *vertical dimension* (Fig. 1) of a river is the interaction between the surface flow of the river channel and cryptic subsurface flows in the alluvium (Hynes 1983, Ward 1989). This vertical connectivity also extends laterally from the river channel into riparian zones and floodplains (Stanford & Ward 1988). The *hyporheic zone* (Fig. 1) is the interface where surface and subsurface flows exchange water, solutes and suspended matter (Brunke & Gonser 1997). The *temporal dimension* (Fig. 1) describes the temporal variation of rivers (Ward 1989), which occurs over both long and short time scales, from diurnal cycles to glaciations and other geological events (Allan & Castillo 2007). Rivers are self-organizing systems which evolve over geologic time, as they strive towards states of equilibrium (Schumm 1973). This inherent behavior is mediated through fluvial processes, which in turn are controlled by physical laws such as slope and alluvium grain-size (Montgomery & Buffington 1997). While the trajectory towards a steady state may be predictable and gradual, it may also be abrupt (Schumm 1973). Extreme floods or external stochastic events may force a river to adjust the trajectory from one stable-state and shift towards a new equilibrium and the subsequent reshaping of the river (Hooke 2007, Boulton *et al.* 2014, Baynes *et al.* 2015). The dynamics of meandering (changes in meander bend sinuosity, migration and cut-off) is a classic example of self-organization and the evolution of river channels (Hooke 2007, Schwenk *et al.* 2015). Furthermore, fluctuations in flow and water temperature may magnify the temporal variability of river ecosystems (Mulholland & Hill 1997, Shore *et al.* 2017). For example, the majority of yearly nutrient exports may occur during high flows over a period of less than two weeks (Meyer & Likens 1979). Flow and water temperature also regulate the timing of phenological events such as fish migrations and the emergence of aquatic insects (Boerger 1981, Manhard *et al.* 2017). Finally, as variations in flow cause the river channel to contract and expand, the level of lateral and vertical connectivity may vary spatiotemporally (Hynes 1983, Junk *et al.* 1989). For instance, the groundwater table may vary with seasonal weather events and may shift the spatial extent of the hyporheic zone and thus the level of exchange across the interface (Hynes 1983).

The hyporheic zone

The hyporheic zone (HZ) (Fig. 1) is a key element of riverine ecosystems, connecting surface and subsurface flows through the exchange of water, organic matter (including organisms), nutrients and other materials (Boulton *et al.* 1998, Boano *et al.* 2014). Various definitions of the HZ exist (see White 1993 & Gooseff 2010). One definition by Boulton *et al.* (1998) states that “*the hyporheic zone can be defined as a spatially fluctuating ecotone between the surface stream and the deep groundwater where important ecological processes and their requirements and products are influenced at a number of scales by water movement, permeability, substrate particle size, resident biota, and the physiochemical features of the overlying stream and adjacent aquifers*” (Boulton *et al.* 1998).

The HZ is characterized by the transition from turbulent unconstrained surface flow to subsurface interstitial flow in porous medium, permanent darkness, longer water residency time and a more stable environment in regards of temperature fluctuations and sediment mobilization (Brunke & Gonser 1997, Boulton *et al.* 1998). Another defining feature of the HZ is the vertical gradients in parameters such as temperature, dissolved oxygen and ion concentration. Compared to surface flow, hyporheic water generally have different temperature and dissolved oxygen regimes, and a higher concentration of ions (Boulton *et al.* 1998). Consequently, hyporheic exchange can be important for regulating nutrient cycling and temperature in the river (Brunke & Gonser 1997). It is also important to note that the HZ differs from groundwater environments (Boulton *et al.* 2006).

Groundwater and river systems are connected via both vertical and lateral hyporheic flow paths in riverbeds, stream banks, riparian zones and beyond into the floodplains (Hill *et al.* 1998, Boano *et al.* 2014) (Fig. 1). Vertical and lateral hyporheic exchange flows are formed where in-stream objects or irregularities of the riverbed cause pressure differentiations (Thibodeaux & Boyle 1987, Storey *et al.* 2003, Boano *et al.* 2014). Pressure drops at nested topographical high points, forcing surface waters into the alluvium where it will follow cryptic hyporheic flow paths and exit the HZ at elevation low points (Fig. 1), e.g. a pool downstream of a riffle (Harvey & Bencala 1993, Gooseff *et al.* 2006).

Areas where surface waters enter the HZ are termed downwelling zones, while upwelling zones are areas where hyporheic water re-enters the river channel (Brunke & Gonser 1997, Boulton *et al.* 1998) (Fig. concept). Large-scale hyporheic flow paths and the spatial extent of the HZ are determined by the permeability and composition of the subsurface lithology and alluvium (Stanford & Ward 1988, Wondzell 2011). For example, upwelling may occur in areas where hyporheic flow in highly permeable alluvium meets impermeable bedrock (Stanford & Ward 1988). The HZ can extend laterally up to 2 km from the river channel in high gradient rivers with coarse alluvium, while it can be limited to a thin layer just below the riverbed in low gradient rivers with fine alluvium and low permeability (Stanford & Ward 1988, Wondzell 2011). Furthermore, discharge and water residence time are two important regulatory factors of the HZ (Boulton *et al.* 1998, Wondzell 2011, Zarnetske *et al.* 2011). Discharge controls the hyporheic turnover length of a river, which can be defined as the average distance the channel flow is required to travel in the HZ before complete hyporheic mixing occurs (Wondzell 2011). In general, average turnover length is shorter in small rivers compared to large rivers, because discharge is positively correlated to stream size and turnover length (Wondzell 2011). Turnover length controls the rate of hyporheic exchange and subsequently the relative importance of

the HZ in regard to its influence on river ecosystem processes such as biogeochemical cycling (Peterson *et al.* 2001, Kasahara & Wondzell 2003).

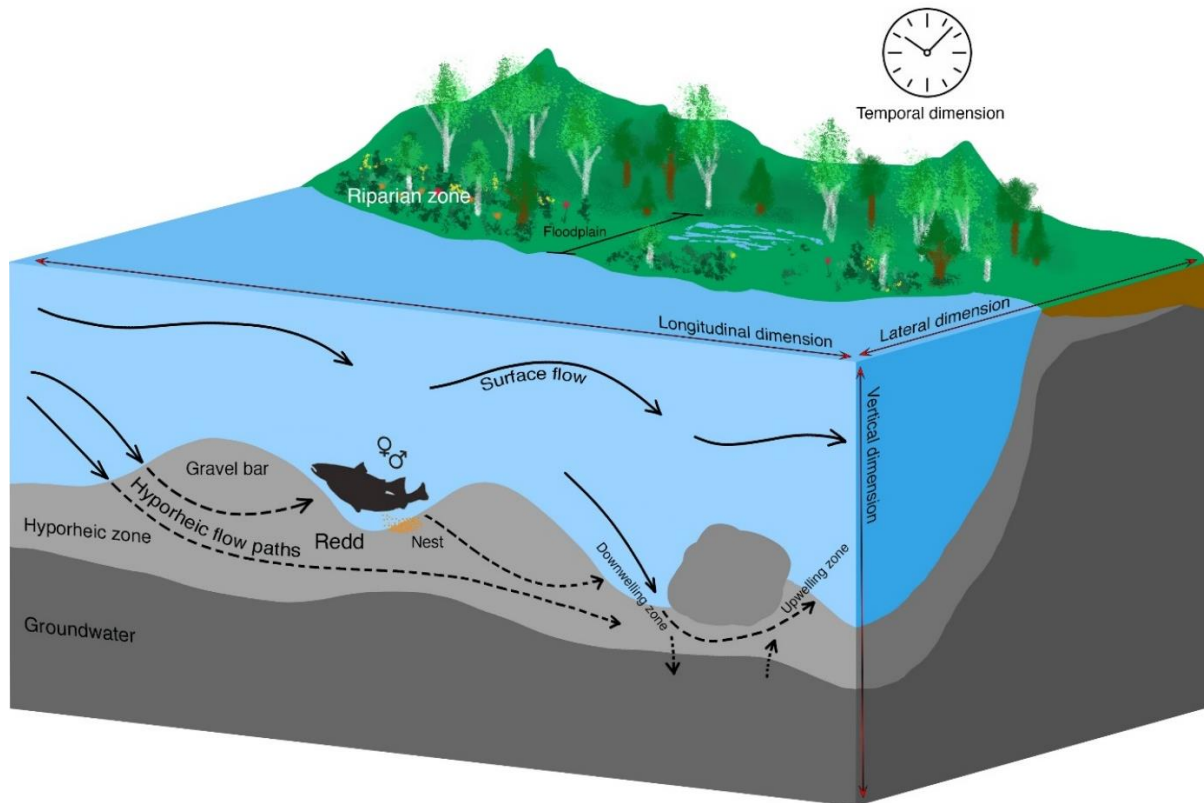


Figure 1. Conceptual illustration describing the four-dimensional nature of river ecosystems with extra focus on the hyporheic zone (HZ). Dashed lines show hyporheic flow paths while the arrows indicate the direction of flow. The two fishes illustrate a male and female salmon spawning in a redd excavated in a gravel bar.

Furthermore, water residence time in the HZ is a vital regulatory factor that affects dissolved oxygen levels and metabolism in the hyporheic environment (Zarnetske *et al.* 2011). Water residence time depends on the permeability of the substrate and the arrangement of hyporheic flow paths (Stanford & Ward 1988, Boulton *et al.* 1998). Short water residence time will result in aerobic conditions but low decomposition rate. In contrast, long water residence time allow a higher rate of decomposition, resulting in low oxygen or even anaerobic conditions where microbial communities may thrive (Boulton *et al.* 1998, Zarnetske *et al.* 2011).

Without insolation, hyporheic food webs are based on microbial decomposition of organic matter (Feris *et al.* 2003). Microbial communities of the HZ are dominated by bacteria, which are of fundamental importance for ecosystem functioning in rivers and streams (Findlay 2010). Denitrifying bacteria is a group of bacteria that can transform NO_3^- to N_2 under anaerobic conditions, permanently removing N from the river system (Findlay 2010). Microbes are therefore vital for biogeochemical cycling in rivers, on average transforming 50% of N input to N_2 through denitrification (Galloway *et al.* 2004). Nitrification is another bacterial mediated process, where NH_4^+ is transformed to NO_3^- under aerobic conditions (Zarnetske *et al.* 2011). Structures such as a gravel bars may have aerobic conditions on the upstream side of the structure where NH_4^+ is transformed to NO_3^- , which is then transformed to N_2 and removed from the system if oxygen is depleted along the hyporheic flow path towards the downstream side of the gravel bar (Zarnetske *et al.* 2011). Nitrification and denitrification are coupled and spatially correlated to the aerobic environments of downwelling zones and anaerobic

environments of upwelling zones, respectively (Zarnetske *et al.* 2011). Upwelling zones with high production of NO_3^- can be hotspots for algae, macrophytes and invertebrates, while downwelling zones can be hotspots for N removal if oxygen is depleted along the hyporheic flow path (Findlay 2010, Zarnetske *et al.* 2011). Furthermore, hyporheic invertebrate communities (hyporheos) have important functions in the HZ, e.g. bioturbation, pelletization and consumption of detritus and microbes (Boulton 2007). The HZ also functions as a thermal refuge for invertebrates and fish when conditions are unfavorable in the surface environment (Ebersole *et al.* 2003, Maazouzi *et al.* 2017). The protected environment of the HZ is utilized by salmonids who bury their eggs in the riverbed during spawning (DeVries 1997).

1.1.2 Atlantic salmon

The Atlantic salmon (*S. salar*) (Fig. 2) is one of the most iconic and well-studied fish species on Earth (Jonsson & Jonsson 2011a). It belongs to the *Salmo* genus along with its closest relative, the brown trout (*Salmo trutta*). Salmon holds high economic and social values, such as commercial and recreational fishing, tourism opportunities and cultural heritage among local and indigenous people (Myrvold *et al.* 2019, Carothers *et al.* 2021). Salmon is considered a keystone species because of the complex life-history, involving migration between freshwater and marine environments (Willson & Halupka 1995, Jonsson & Jonsson 2011a). During the migrations, salmon transports marine-derived nutrients to their natal rivers, increasing the productivity of freshwater ecosystems (McLennan *et al.* 2019). Salmon also impact marine and freshwater food webs through trophic interactions (Willson & Halupka 1995, Suuronen & Lehtonen 2012, Samways *et al.* 2017). Salmon is also a host during the parasitic larval stage of the threatened freshwater pearl mussel (*Margaritifera margaritifera*), another iconic keystone species which is dependent on salmon (Geist 2010). Furthermore, salmon is an ecosystem engineer who alters the structure and size distribution of the alluvium when they excavate nests during spawning, thus affecting the dynamics of the HZ (Field-Dodgson 1987, Kondolf *et al.* 1993).

Geographical distribution

The native distribution range of the Atlantic salmon (hereafter salmon) spans over the Atlantic Ocean from eastern North America to Iceland, over the British Isles, Scandinavia and all the way to the Barents Sea around Svalbard and northern Russia (MacCrimmon & Gots 1979). The southern limit is in the northwestern parts of Spain and Portugal. The current distribution range is influenced by the latest glaciation which salmon endured in several glacial refuges, from where they dispersed during the deglaciation (Tonteri *et al.* 2005). Salmon is genetically and geographically separated into three main groups, the West Atlantic group in North America, the East Atlantic group in Western Europe and the Baltic Group in the Baltic Sea basin (Jonsson & Jonsson 2011b). The Baltic Group is youngest of the three, as the Baltic Sea began to form ca 16 ka BP when the Weichselian ice sheet had retreated from southern Scandinavia (Andrén *et al.* 2011). Moreover, some salmon populations were isolated in freshwater lakes during the deglaciation (Hutchings *et al.* 2019), e.g. the landlocked population in Lake Vänern (Ros 1981).

Life-history

The life-history of a salmon is a complex story. Most salmon are anadromous, meaning they are born in freshwater where they also stay as juveniles, but migrate to marine environments to grow and mature, before returning to freshwater to spawn as adults. Some populations however complete the life cycle exclusively in freshwater or migrate to brackish environments such as the Baltic Sea (Aas *et al.* 2010, Hutchings *et al.* 2019).



Figure 2. Atlantic salmon in three different life stages. Top left: the eyed egg-stage just prior to planting in Gysinge. Top right: alevins (recently hatched juveniles) recovered from the sampling units in Gysinge. The maternal yolk sacs are still clearly visible. Bottom: adult female salmon with a length of 110 cm and weight of 11 kg captured in Kungsådran at Älvkarleby. Note the absence of an adipose fin, indicating an individual of stocked origin. Fin-clipping is a common marking method for sea migrating hatchery fish (Petersson *et al.* 2014).

Salmon spawn in pairs during the autumn or winter, with populations in the northern geographical range spawning earlier than southern populations (Aas *et al.* 2010). During spawning, the female turns to her side and uses her tail and body to excavate one or several redds in the substrate of the riverbed. A redd is the approximal area of gravel containing the nests of one female (Fig. 1), and a nest is a pocket in the substrate where a female deposits her eggs (Crisp & Carling 1989). Salmonid females may be able to probe the quality of the redd by pressing the belly tight against the bottom of the redd and lowering the anal fin into the substrate (Tautz & Groot 1975, Jonsson & Jonsson 2011a). If satisfied, the female deposits her eggs and the male fertilizes them before the female covers the nests using surrounding substrate. On average, a female releases 1600-1800 eggs per kg bodyweight (Bardonnnet & Baglinière 2000). The eggs are buried at a depth of 15-30 cm and develop during winter (Crisp & Carling 1989, DeVries 1997). Redds are commonly excavated next to in-stream structures such as gravel bars where hyporheic exchange flows often occur (Fig. 1), which may be beneficial for incubating eggs in terms of oxygen supply (Baxter & Hauer 2000, Bowerman *et al.* 2014, Harrison *et al.* 2019). The eggs will hatch during the following spring, the exact timing is controlled by water temperature (Crisp 1988).

The emerging alevins (newly hatched individuals) (Fig. 2) are still relying on the maternal yolk sacs and will remain hidden in the riverbed until the yolk sacs has been absorbed. Then, the alevins will make their way up to the surface flow of river channel to take up position in shallow, low velocity habitats (Jonsson & Jonsson 2011c). This transitional stage is termed the swim-up. It is a bottleneck (critical phase) in salmon ontogeny and is characterized by high mortality (up to 90%) because of the exposure to a novel environment, displacement and the shift to exogenous feeding (Armstrong *et al.* 2003, Armstrong & Nislow 2006, Jonsson & Jonsson 2011c). The individuals who successfully makes the transition have reached the parr-stage, which will last for a couple of years until the parrs transform into smolts. Smoltification (parr-smolt transformation) occurs when parr have reached a size of 8-12 cm (Jonsson & Jonsson 2011d). The transformation is a reversible physiological adaptation that prepares the salmon for the marine environment and long-range migrations. Smoltification involves changes in morphology, salinity tolerance, behavior and pigmentation (Jonsson & Jonsson 2011d). The seaward smolt migration from freshwater to the sea mainly occurs in spring or early summer (Aas *et al.* 2010, Jonsson & Jonsson 2011d).

When the smolts reach the sea, they are called post-smolts, and will pass through another ontogenetic bottleneck as they migrate to another novel environment. Marine mortality typically exceeds 90% (Jonsson & Jonsson 2011c) and is at its highest during the first days of smolt migrations, when the daily predation rate may reach 25% (Dieperink *et al.* 2002). In the marine environment post-smolts shift to a mainly piscivorous diet and grow quickly to avoid predation. Baltic populations migrate to feeding grounds in the southern Baltic Sea where herring (*Clupea harengus*) is the main prey item (Jacobson *et al.* 2020). Most individuals spend 1 to 4+ years at sea, during which time they will increase in weight from 0.05 kg up to 25 kg (Aas *et al.* 2010). When sexually mature, salmon may migrate hundreds of kilometers back to their natal rivers to spawn. The homing behavior enables salmonids to find their way back to the river where they were born (Salmenkova 2017). Homing is the driving mechanism which maintains and develops local adaptations in salmon populations (Taylor 1991, Garcia de Leaniz *et al.* 2007). Atlantic salmon is iteroparous, meaning they can migrate and spawn multiple times unlike Pacific salmon (Fleming 1996).

Requirements for spawning, embryonal survival and development

Salmon select spawning sites based on flow conditions such as water depth and velocity, and the size and quality of the substrate (Louhi *et al.* 2008, Harrison *et al.* 2019). Because of the specific requirements, suitable spawning sites may be a limiting factor for population sustainability (Louhi *et al.* 2008). Spawning salmon prefer water depths of 20-55 cm and substrate sizes between 16 and 128 mm (Louhi *et al.* 2008). The range is partly explained by the natural variation in river channel characteristics within and between rivers, but also that the requirements are size-dependent and scales with female size. Substrate size, water velocity and depth, number and size of eggs, redd size, burial depth, and breeding success is positively correlated to the size of the female (Crisp & Carling 1989, Kondolf & Wolman 1993, DeVries 1997, Aas *et al.* 2010). The development and survival of salmonid eggs and alevins are highly dependent on interstitial water conditions (Sternecker *et al.* 2013a) where temperature, oxygen and pH are critical factors (Finn 2007). Temperature is the main driver of embryonic development and controls the timing of hatching and swim-up (Crisp 1988, Hannah *et al.* 2004, Sternecker *et al.* 2013a, Smialek *et al.* 2021). Salmon have high demands on dissolved oxygen concentrations in the hyporheic environment, but the demands vary with developmental stage (Armstrong *et al.* 2003, Finn 2007, Smialek *et al.* 2021). Newly fertilized eggs are more tolerant than eggs that are close to hatching, which are sensitive to dissolved oxygen concentrations less than 7 mg/L (Armstrong *et al.* 2003, Finn 2007, Louhi *et al.* 2008, Smialek *et al.* 2021).

Prolonged periods of low concentrations of dissolved oxygen can cause direct mortality or have sublethal effects (Malcolm *et al.* 2003, Youngson *et al.* 2004, Finn 2007, Sear *et al.* 2017, Lavery & Cunjak 2019). However, the eggs may tolerate shorter periods of anoxia (Finn 2007, Côte *et al.* 2012) and even conditions in desiccated iced-covered redds (Casas-Mulet *et al.* 2015).

The survival of salmonid eggs has been shown to be positively correlated to the strength of downwelling at spawning sites, as it increases oxygen concentrations in the redd environment (Bowerman *et al.* 2014). Upwelling of long-residence groundwater can be harmful as it tends to be low in dissolved oxygen (Malcolm *et al.* 2003, Youngson *et al.* 2004). Upwelling groundwater also tends to be warmer than surface waters during incubation, thus accelerating embryo growth and impacting the timing of emergence (Curry *et al.* 1995, Acornley 1999). Depending on flow conditions and food availability, early emergence can increase the growth rate as a result of reduced competition, but early emerging juveniles may also be exposed to unfavorable conditions such as reduced food availability and increased risk of displacement due to high flows (Acornley 1999). Furthermore, infiltration of fine sediment into the redd can cause asphyxiation and entombment, which are suggested to be the two main drivers of embryonic mortality (Greig *et al.* 2007). Large particles such as sand may clog the upper layers of the redd and entomb alevins, while the presence of small particles like clay can reduce both oxygen supply and the rate of exchange across the egg membrane (Greig *et al.* 2005, Greig *et al.* 2007). The negative effects of fine sediment on salmonid egg survival have been well-studied (Chapman 1988, Soulsby *et al.* 2001, Malcolm *et al.* 2003, Greig *et al.* 2005, Greig *et al.* 2007, Bowerman *et al.* 2014). It is important to emphasize that mortality among salmonids in early life-stages is not caused by a single factor but a combination of factors (Lavery & Cunjak 2019, Smialek *et al.* 2021).

Salmon can tolerate pH levels between 6 and 9, but higher and lower levels may have indirect or direct toxic effects on salmon in all life-stages (Smialek *et al.* 2021). For example, acidification have caused major die-offs and the loss of salmon in 25 Norwegian rivers (Hesthagen & Hansen 1991). Additionally, pH may affect the solubility of substances which can be toxic to salmon, such as aluminum and ammonia (NH₃) (Finn 2007). Aluminum may be dissolved, leached from soils and flushed into rivers at pH levels below 4.5 (Forseth *et al.* 2017), while the fraction of aquatic NH₃ increase with pH and can reach about 50 % at pH levels around 9 (Emerson *et al.* 1975). NH₃ may cause slowed larval growth and reduced body mass at exposures between 6–180 µg/L NH₃ (Vosyliene & Kazlauskienė 2004), while acute ammonia toxicity has been observed at higher concentrations ranging from 0.16 to 1.1 mg/L (Thurston & Russo 1983). However, salmonid eggs have a high tolerance to ammonia as the embryos are able to detoxify ammonia using physiological mechanisms (Vedel *et al.* 1998). These mechanisms are however lost in later life-stages, making salmon more vulnerable to ammonia in later life-stages (Vedel *et al.* 1998).

1.1.3 Human activities and river ecosystems

Freshwater ecosystems have provided human civilizations with vital ecosystem services throughout history (Limburg 2009, Hanna *et al.* 2018), but the high and increasing human demand on these ecosystems are threatening biodiversity and the provisioning of services (Vörösmarty *et al.* 2010, Dudgeon 2019). Human activities are causing ecosystem degradation, leading to population declines and increasing risks of extinctions among freshwater organisms (Dudgeon *et al.* 2006, Vörösmarty *et al.* 2010, Reid *et al.* 2019, Albert *et al.* 2021). Moreover, historical events such as the acid rains in the middle of the 20th century (Rothschild 2019) and timber floating during the 19th and 20th centuries (Törnlund & Östlund 2002, Nilsson *et al.* 2005a) are still affecting river ecosystems through legacy effects. Habitat destruction and degradation, overexploitation, flow modification, pollution and invasions by exotic species are regarded as the most acute anthropogenic stressors (Fig. 3) (Dudgeon *et al.* 2006). Numerous additional threats contribute to the degradation of freshwater ecosystems (Fig. 3) (Reid *et al.* 2019). Damming of rivers for the sake of generating hydropower have been suggested to be the most destructive human activity in river ecosystems (Nilsson *et al.* 2005b, Liermann *et al.* 2012, Lenders *et al.* 2016, Chen & Olden 2017, Rehbein *et al.* 2020). Hydropower has a wide range of effects on river ecosystems through (but not limited to) flow modification (Nilsson *et al.* 2005b), fragmentation of the river continuum (Bellard & Hugueny 2020, Barbarossa *et al.* 2020, Belletti *et al.* 2020), blocking of migration routes (Liermann *et al.* 2012) and geomorphic changes to the river channel (Williams & Wolman 1984). On top of this, rivers are affected by historical and ongoing land-use within the catchment, such as agriculture, forestry and water extraction (Harding *et al.* 1998, Carignan & Steedman 2000, Allan 2004). Furthermore, stressors interact with each other and do not act independently (Birk *et al.* 2020). Multiple stressors interacting may have antagonistic, synergistic, additive or reversed effects, and are known to cause unpredictable ecosystem responses, also known as ecological surprises (Jackson *et al.* 2016). However, the interactions and effects of multiple stressors are not fully understood (Foster *et al.* 2016, Pistocchi *et al.* 2017).

Ecosystem effects

In short, human activities encroach on the highly complex riverine landscape, turning it into a more homogenous environment with reduced niche variation (Peipoch *et al.* 2015). Some human activities such as pollution may not reduce the physical variation of the environment, but could nevertheless lead to simplification through other mechanisms, such as altered species compositions due to extirpations or stress responses (Peipoch *et al.* 2015). Ecological simplification could threaten the four-dimensional nature of rivers, resulting in loss of biodiversity and altered ecosystem functioning (Fagan 2002, Boulton 2007, Eloegi & Sabater 2013, Peipoch *et al.* 2015). Additionally, climate change will have a wide array of effects on freshwater ecosystems (Palmer *et al.* 2008, Whitehead *et al.* 2009, Friberg *et al.* 2013, Tonkin 2022). Precipitation in boreal regions is likely to increase with a changing climate (IPCC 2021), causing alterations to river flow regimes (Blöschl *et al.* 2019, Rydén 2022, Tonkin 2022), with possible implications on habitat and environmental conditions which are crucial to salmon (Jonsson & Jonsson 2011e).

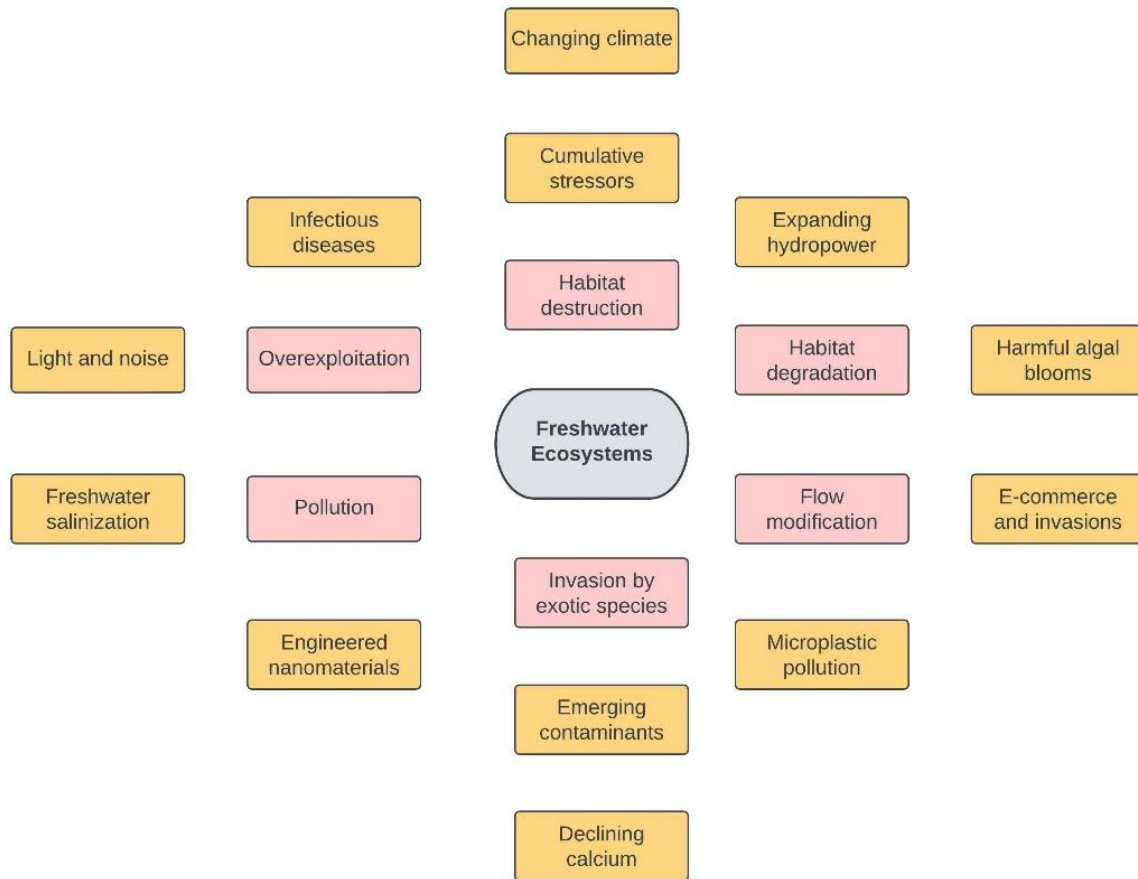


Figure 3. Anthropogenic stressors affecting freshwater ecosystems. Boxes in red are the most acute stressors according to Dudgeon *et al.* (2006). The surrounding boxes are the emerging threats identified by Reid *et al.* (2019). Adapted from Dudgeon *et al.* (2006) and Reid *et al.* (2019).

As a species with a complex life-history, salmon serves as the perfect model organism to illustrate some (but far from all) of the effects of human disturbance in freshwater ecosystems. Human activities are driving the decline of salmon populations by degrading both the freshwater and marine habitats which salmon depend on (Limburg & Waldman 2009, Lenders *et al.* 2016, Forseth *et al.* 2017, Reid *et al.* 2019, Deinet *et al.* 2020). Note that marine disturbances such as stock exploitations (Mäntyniemi *et al.* 2012), salmon farming (Lund & Heggberget 1992, Diserud *et al.* 2022), disease and pollution (Larsson *et al.* 1996, Koski *et al.* 1999, Keinänen *et al.* 2018) are not presented here, but are very much affecting salmon populations. Forseth *et al.* (2017) reviewed the major anthropogenic factors threatening Norwegian salmon populations (Fig. 4).

Migration barriers such as dams are blocking migration routes, making salmon unable to reach their spawning grounds to complete their lifecycle (Limburg & Waldman 2009, Liermann *et al.* 2012). To maximize power generation, hydropower dams are constructed in streaming habitats where the energy of flow is high (Hall *et al.* 2011). Construction of dams lead to loss and degradation of habitats. River sections upstream of dams are inundated and transformed into lake-like environments, while downstream sections suffer from reduced wet areas (Baxter 1977, Baran *et al.* 1995).

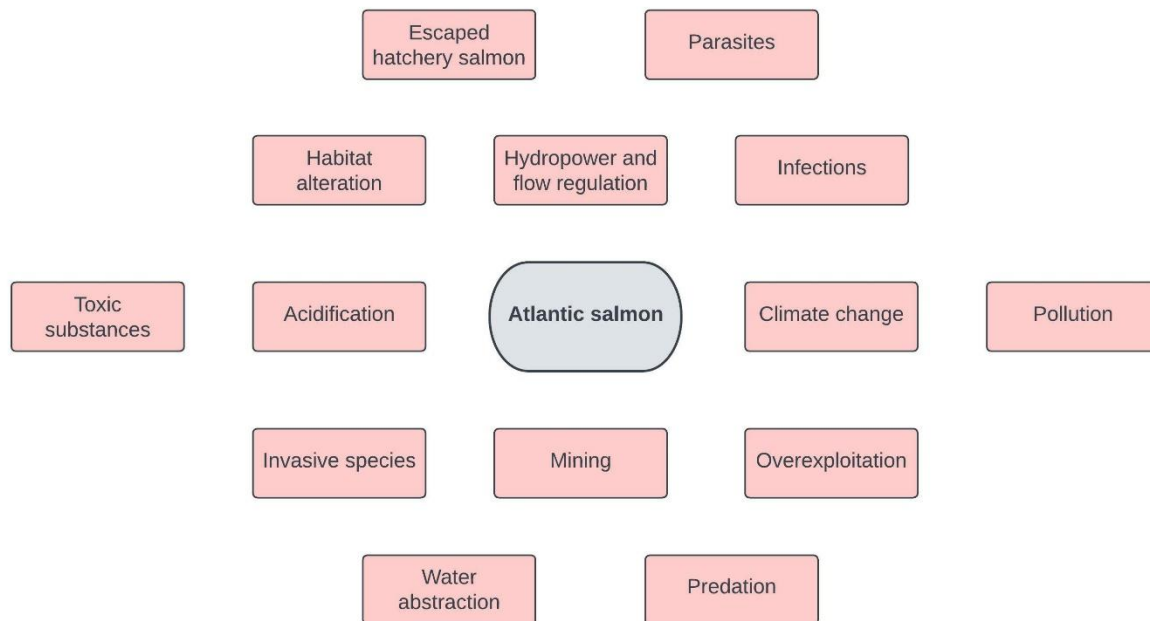


Figure 4. Anthropogenic factors threatening Norwegian salmon populations according to Forseth *et al.* (2017). Escaped hatchery salmon threaten wild populations by hybridization between salmon of wild and hatchery origin, causing loss of genetic integrity in wild populations. Parasites spread from salmon farms and infect wild populations, increasing mortality rates up to over 90 % in juvenile salmon (Forseth *et al.* 2017). The other threats are presented in falling order of impact.

Furthermore, the regulation of flow at dams will erode the natural flow regime of a river, leading to widespread ecological consequences (Baxter 1977, Baran *et al.* 1995, Ligon *et al.* 1995, Poff *et al.* 1997, Parasiewicz *et al.* 1998, Nyberg *et al.* 2008, Vollset *et al.* 2016). Flow regulation may degrade habitats and make them inaccessible due to alternating episodes of high and low flows. This can result in behavioral changes in salmon, with potentially negative impacts on fitness (Parasiewicz *et al.* 1998, Saltveit *et al.* 2001, Jensen 2003, Vollset *et al.* 2016). For example, short-term regulation has been shown to interfere with spawning, forcing females to excavate redds at suboptimal locations where the offspring have a lower chance of survival (Vollset *et al.* 2016). Minimal flow may dewater parts of the river channel, resulting in stranding of juvenile salmon (Hvidsten 1985, Young *et al.* 2011), and expose eggs and alevins to draught or freezing conditions (Becker & Neitzel 1985, Casas-Mulet *et al.* 2015). Peak flows can flush away eggs or displace juvenile fish (Parasiewicz *et al.* 1998, Young *et al.* 2011). Additionally, damming and unnatural flow regimes alters the flux of sediments when it is trapped at upstream sections of dams, while downstream sections are starved (Williams & Wolman 1984, Ligon *et al.* 1995). Subsequent changes in erosion and deposition dynamics could alter river channel morphology, impacting habitat availability and quality (Juracek & Fitzpatrick 2022). Flow regulation have also been shown to impact hyporheic water quality, with potentially negative effects on incubating salmonid eggs (Nyberg *et al.* 2008).

Additionally, ongoing and historical land use, such as agriculture and forestry, may pollute rivers and degrade salmon habitat (Soulsby *et al.* 2001, Heaney *et al.* 2001, Mellina & Hinch 2009, Löfgren *et al.* 2009, Collins *et al.* 2014, Eklöf *et al.* 2016). Removal of riparian vegetation can negate the buffering capacity against sedimentation of clay particles (Collins *et al.* 2010) which may suffocate salmon embryos (Greig *et al.* 2007), reduce refugia for juvenile salmonids (Heifetz *et al.* 1986) and impact salmonid fitness and habitat use if thermal conditions are

affected negatively (Dan Moore *et al.* 2005, Jonsson & Jonsson 2011c, O'Sullivan *et al.*). Clear-cutting, soil preparation and land drainage may alter flow regimes and sediment dynamics. The above mentioned forest management measures has been shown to increase peak flows (Robinson *et al.* 2003, Buttle *et al.* 2018) and input of fine sediment (Nieminen *et al.* 2017), both which may be harmful to early life-stages of salmonids (Chapman 1988, Parasiewicz *et al.* 1998, Soulsby *et al.* 2001, Greig *et al.* 2005, Greig *et al.* 2007, Young *et al.* 2011, Bowerman *et al.* 2014). During the timber floating era, many rivers and streams were physically transformed. Main channels were straightened, side channels were shut off and in-stream objects such as large boulders and woody debris were removed (Törnlund & Östlund 2002, Nilsson *et al.* 2005a). Alterations of such nature have been shown to result in loss of salmonid spawning and rearing habitats (Scruton *et al.* 1998, Jutila *et al.* 1998), and may be responsible for major declines in Baltic salmon populations (Nilsson *et al.* 2005a).

Long-range migratory fish species like salmon are disproportionately threatened as they are affected by human activities in both freshwater and marine environments (Deinet *et al.* 2020). There has been a $\approx 93\%$ average decline in European freshwater migratory fish species from 1970 to 2016 (Deinet *et al.* 2020). Salmon populations throughout their distribution area are at historically low levels (Limburg & Waldman 2009, Lenders *et al.* 2016), including the Baltic Sea group (McKinnell 1999). However, over the last decades, efforts are increasing to restore degraded river ecosystems and strengthen salmon populations (Palmer *et al.* 2007, Jähnig *et al.* 2009, Piégay *et al.* 2020).

1.1.4 River restoration

Since the implementation of EU Water Framework Directive (Directive 2000/60/EC) and other policies aiming to improve the status of freshwater ecosystems, billions of Euros and considerable efforts are globally invested into restoring rivers (Palmer *et al.* 2007, Muhar *et al.* 2016, Roni 2019). River restoration is both a field of science and a practical method with the aims of improving hydrologic, geomorphic and ecological conditions of rivers (Wohl *et al.* 2015). From the beginning of the 1980s, many restoration projects had a form-based approach with focus on creating or improving fish habitats, rather than focusing on the recovery of lost ecosystem functions and processes (Wohl *et al.* 2015). Currently, a process-based approach is more common, where lost functions and processes are recovered through improved lateral and longitudinal connectivity, altered flow conditions and enhanced freshwater communities (Wohl *et al.* 2015). Even if the field of river restoration has evolved, important aspects such as climate change, land use, multiple stressors, vertical connectivity and whole-catchment restoration are often overlooked (Boulton 2007, Beechie *et al.* 2013, Göthe *et al.* 2019, Birk *et al.* 2020, Diefenderfer *et al.* 2020). Implemented restoration measures varies between projects depending on stakeholders involved, restoration goals and level of ecosystem degradation (Palmer *et al.* 2016). Common examples of restoration measures are modifications to channel morphology and in-stream objects, dam removal and environmental flow control (Fig. 5) (Wohl *et al.* 2005, Roni *et al.* 2008, Angus Webb *et al.* 2013, Wohl *et al.* 2015). Good-practice river restoration calls for resilient and self-sustained measures (Palmer *et al.* 2005, Muhar *et al.* 2016). Furthermore, fishery managers commonly use augmentation or cleaning of spawning substrate (Wheaton *et al.* 2004, Barlaup *et al.* 2008, Pander *et al.* 2015, Pulg *et al.* 2022), stocking of hatchery reared juveniles (Petersson *et al.* 1996, Dannewitz *et al.* 2004, Jonsson & Jonsson

2011f) and egg planting (Johnson 2004, Saltveit & Brabrand 2013, Syrjänen *et al.* 2015, Barlaup & Moen 2001) to enhance threatened salmon populations.

Restoration measures such as modifications of channel morphology often increase habitat heterogeneity (Lepori *et al.* 2005, Nilsson *et al.* 2005a, Jähnig *et al.* 2010, Lorenz & Feld 2013) and may enhance salmonid production, but the results are inconclusive (Louhi *et al.* 2016, Foote *et al.* 2020). The response from river biota is generally highly variable, often slow or even non-existent (Roni *et al.* 2008, Nilsson *et al.* 2015, Roni 2019, Foote *et al.* 2020). Additionally, the response varies along the river continuum and depends on factors such as the intensity of land use and time since restoration (Manfrin *et al.* 2019). Positive effects on reach-scale can be masked by intense riparian land use and low-quality habitats upstream of the restored site (Lorenz & Feld 2013). Manfrin *et al.* (2019) showed that communities shifted towards opportunists during the first 5 years following restoration, and a subsequent shift back to communities in equilibrium. This indicates that the years following a restoration effort could be characterized as a recovery period after a disturbance event and could help explain the lack of response in monitored biota, especially since restoration projects monitor for less than five years (Foote *et al.* 2020). According to Louhi *et al.* (2016), a minimum of 10 years of monitoring is required to evaluate the response of biota. The lack of response from biota have also been suggested to be a result of insufficient monitoring and evaluation (Palmer *et al.* 2014, Wohl *et al.* 2015, Louhi *et al.* 2016). Many restoration projects lack or have poorly designed methods for evaluation and long-term monitoring, mainly because it is not prioritized and is in need of standardized procedures (Palmer *et al.* 2014, Wohl *et al.* 2015, Nilsson *et al.* 2016). Studies have shown that the evaluation of success is inconsistent between restoration projects (Morandi *et al.* 2014, Kurth & Schirmer 2014), and is often based on gut-feeling rather than empirical data and ecological indicators (Jähnig *et al.* 2011, Weber & Peter 2011).

The uncertainties regarding the effectiveness of river restoration calls for improved practices and tools (Jähnig *et al.* 2011, Morandi *et al.* 2014, Marttila *et al.* 2016, Nilsson *et al.* 2016, Louhi *et al.* 2016, Rubin *et al.* 2017, Foote *et al.* 2020). Furthermore, different stakeholders may have different definitions of restoration, causing confusion among practitioners and researchers (Wohl *et al.* 2015). Ecological restoration is another term used, again with different definitions, depending on restoration goals and reference system (Wohl *et al.* 2015, Palmer *et al.* 2016, Gann *et al.* 2019).

Reference systems could be pristine natural systems or semi-natural systems affected only by traditional land use (Gann *et al.* 2019). One hardline definition of ecological restoration is a full recovery of a degraded system to a pristine condition (Gann *et al.* 2019), while other definitions would allow for a partial recovery of a degraded system to an acceptable condition (Palmer *et al.* 2016). Wohl *et al.* (2015) suggests that there is a need to “*distinguish ecological river restoration that assists the recovery of ecological integrity in a degraded watershed by reestablishing the processes necessary to support the natural ecosystem within the watershed from restoration intended for other outcomes such as enhanced recreation*”. For a reader this might seem confusing, but it demonstrates that river restoration ecology is a relatively new field of science where concepts, terms and definitions have not been fully developed (Graf 2008). Such uncertainty in communication could hamper further development (Suddaby 2010).



Figure 5. River restoration in practice, Ängerån (Gävleborg county). *Top picture:* an excavator in the process of returning river-derived material which was used to build an artificial levee during the timber floating era. The goal with removing artificial levees was to restore the lateral connectivity and increase the wet area of the river. Trees growing on the levee were used as large woody debris in the river channel. *Bottom left picture:* Before restoration. A dam sealing off a large side-channel was built to concentrate the timber to one channel. All vegetation had been removed from the dam by the time the picture was taken. *Bottom right picture:* After restoration. The dam construction has been opened up and water is flowing in the side channel again. In order to retain water levels in sections located upstream, a local knick-point was constructed using the material from the dam. Full recovery was not possible in this case since the solid bedrock which retained the water level in the past was blasted to fragments using black powder and dynamite. The fragments were then used to construct the dam. Remnants of intact bedrock can be seen in the bottom right corner.

1.2 Aims

This study will attempt to further develop tools based on Whitlock (1995) and Pander *et al.* (2009) for evaluation and monitoring of restoration success in regards of ecosystem function (functionality of spawning grounds). A combination of abiotic and biotic variables will be used to assess if restoration efforts in lower Dalälven at the Gysinge area have improved the conditions which are critical to salmon in early life-stages. Additionally, the same combination of variables will be used to assess if the conditions in the egg planting containers used by the County Administrative Board of Gävleborg resembles the natural conditions of the riverbed. Pander *et al.* (2009) developed a sampling unit which combines measurements of habitat variables and egg hatching success. Sternecker *et al.* (2013b) then successfully applied the method to assess the functionality of restored spawning grounds in a small subalpine stream. However, the sampling device developed by Pander *et al.* (2009) needs to be constructed from scratch, while other egg incubators such as Whitlock-Vibert boxes (Whitlock 1995) are widely used in river management and readily available for purchase online but lacks components for sampling of hyporheic water. Modifications to the Whitlock-Vibert box may produce an accessible and user-friendly alternative which can be implemented for monitoring and evaluation of restoration success. Therefore, this study could contribute with new insights for monitoring and evaluation of restoration success in other projects. Additionally, the results may provide answers for stakeholders regarding factors which could limit future salmon production in the Gysinge area.

The aims are to evaluate if:

- (1) interstitial water conditions which are critical for the survival and development of salmon eggs and alevins are more favorable at restored sites compared to non-restored sites.
- (2) conditions inside the egg planting containers placed on top of the riverbed resemble the conditions in the interstitial environment of the riverbed, where the eggs would be deposited naturally.

This will be done by testing for differences in dissolved oxygen, water temperature, pH, NH₃, conductivity, egg hatching rate and accumulated clay particles between restored sections, non-restored sections and the egg planting containers at the Gysinge area of Nedre Dalälven. Because the egg planting containers are exposed to surface flow, the most favorable conditions and therefore highest hatching rates are expected in the egg planting containers compared to the conditions and hatching rates at restored and non-restored sections. Since restoration efforts should improve conditions at restored sections, the conditions are expected to be least favorable in non-restored sections, resulting in the lowest hatching rate.

2. Study area

The study area is located in the lower section of river Dalälven (Nedre Dalälven) close to Gysinge and Sevedskvarn villages, situated in central Sweden where the southern border of Gävleborg county and northern border of Uppsala county meet. The climate in this region is temperate, and the vegetation is dominated by boreal and hemiboreal forests. The yearly mean temperature is 6°C and the yearly mean precipitation is 544.7 mm. The growing season is 201 days and days of snow cover is 74 days. The regional bedrock is old (>1.8 billion years) and dominated by intrusive granites and sections of more calcic rich gabbroids. It is a part of the sub-Cambrian peneplane, forming a flat landscape with a difference in elevation of only <20 m. The bedrock in the area is mainly overlain by sand-rich till with postglacial clay and peat infilling depressions. Alluvium is deposited along the well-developed floodplain.

The drainage area of Dalälven is $\approx 28.000 \text{ km}^2$, which is equal to 6% of the total area of Sweden. The drainage area is dominated by forests (72%) followed by wetlands (11%). Lakes and watercourses cover 6% of the drainage area, while agriculture and urban areas corresponds to 3% and 1% respectively. Dalälven is the second longest river in Sweden (520 km) with a yearly mean discharge of $365 \text{ m}^3/\text{s}$ (min $40 \text{ m}^3/\text{s}$, max $2500 \text{ m}^3/\text{s}$). The lower section of Dalälven, (Nedre Dalälven) makes a turn to the northeast close to Avesta in Dalarna county, abandoning the confined river valley. The original river channel which emptied into lake Mälaren was cut off by the esker Badelundaåsen during the last glaciation, sometime around 7 ka BP. Lower Dalälven can therefore be considered a young river in geological terms and is yet to erode a river valley along the flow path. The unique landscape is shaped by eskers and moraines which were deposited at the ice margin in an estuary environment, before being uplifted (Strömberg 1981). Lower Dalälven runs a length of 120 km before discharging into Gävle Bay in the southern Bothnian Sea and is characterized by the succession of large shallow fjards (fjärd in Swedish), followed by short reaches of rapids. Färnebofjärden with over 200 islands is the largest fjard of lower Dalälven and is located just upstream of the study area. Färnebofjärden had an ice cover until March 27th 2022, but a partial ice cover remained in some bays until April 21st. In the study area of Gysinge, a series of islands forces the river channel to split into two main channels. Discharge during the study period varied between $100\text{--}350 \text{ m}^3/\text{s}$ (Fig. 6). The rapids are concentrated around Sevedskvarn to the east of the island Mattön, and around Gysinge to the north of Mattön. Because of the low gradient and unconfined flow, lower Dalälven regularly inundates the surrounding land, forming a dynamic and heterogenous landscape which holds very high nature values.

Färnebofjärden is one of Sweden's national parks and protected by the Ramsar convention. Additionally, lower Dalälven is an UNESCO Biosphere Reserve. The fish community of lower Dalälven consists of over 20 fish species, from salmonids such as grayling (*Thymallus thymallus*), salmon and brown trout (*Salmo trutta*) to different cyprinids and the large-bodied piscivores pike (*Esox Lucius*) and zander (*Sander lucioperca*). Although lower Dalälven holds high nature values, the river is affected by anthropogenic activities such as damming and hydropower production. There are at least 962 dams in the entire Dalälven drainage area, of which 131 are hydropower plants. The hydropower plant closest to Gysinge is located 24 km downstream in Söderfors, while the closest upstream is located in Näs, 28 km from Gysinge. One small-scale hydropower plant is also located in a small side-channel of the Gysinge area. Älvkarleby hydropower plant is situated closest to the river mouth in the Baltic Sea and was completed in 1915. Since then, the migration routes for salmon in Dalälven have been blocked.

Today, the salmon population of Dalälven is confined to a 10 km river stretch downstream the Älvkarleby hydropower plant and is fully sustained by hatchery operations. Furthermore, the river channel at the Gysinge area was modified during the timber floating era, but restoration efforts were made in 2016 and 2018. Future fish passages or other technical solutions could enable migration. Construction of fish passages and other measures will be settled in the ongoing revision of Swedish hydropower plant licenses (Havs- och vattenmyndigheten 2022).

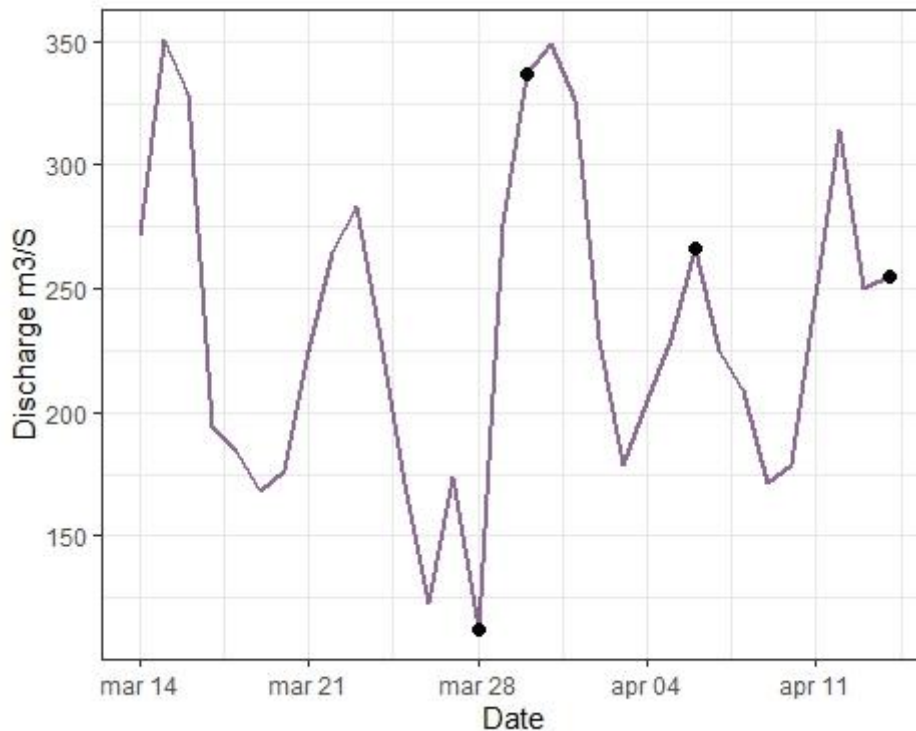


Figure 6. Daily mean discharge (m^3/s) at Näs hydropower plant 28 km upstream of the study area in Gysinge is shown on the Y-axis and date on the X-axis. The observations range from March 14th when egg planting started to April 14th when the final sampling was made. The black circles represent the four sampling occasions.

2.1 Sampling sites

Three sites (1-3) (Fig. 7) in the Gysinge area were identified by having similar hydrological conditions, locations where the County Administrative Board annually placed egg planting containers, and restored and non-restored sections in close proximity of each other and egg planting sites (<200 m). Within these three sites, sampling locations were then determined, resulting in a total of 9 sampling locations (3 restored, 3 non-restored and 3 egg-planting containers) per site (Fig. 8), resulting in a total of 27 sampling locations distributed over all three sites (1-3) (Fig. 7). All sampling locations were located within previously mapped areas that were estimated to be suitable spawning habitats for salmon (Hagelin *et al.* 2018). Restored locations were defined as locations where restoration measures have been performed and gravel augmentations could still be observed, while non-restored locations were defined as sites with suitable spawning substrate, but no implemented restoration measures. Modified Whitlock-Vibert boxes (MWVB) containing salmon eggs were buried in the riverbed or placed in egg-planting containers at each sampling site in all three locations (Fig. 9). Field work was performed between March 14th and May 5th, 2022.

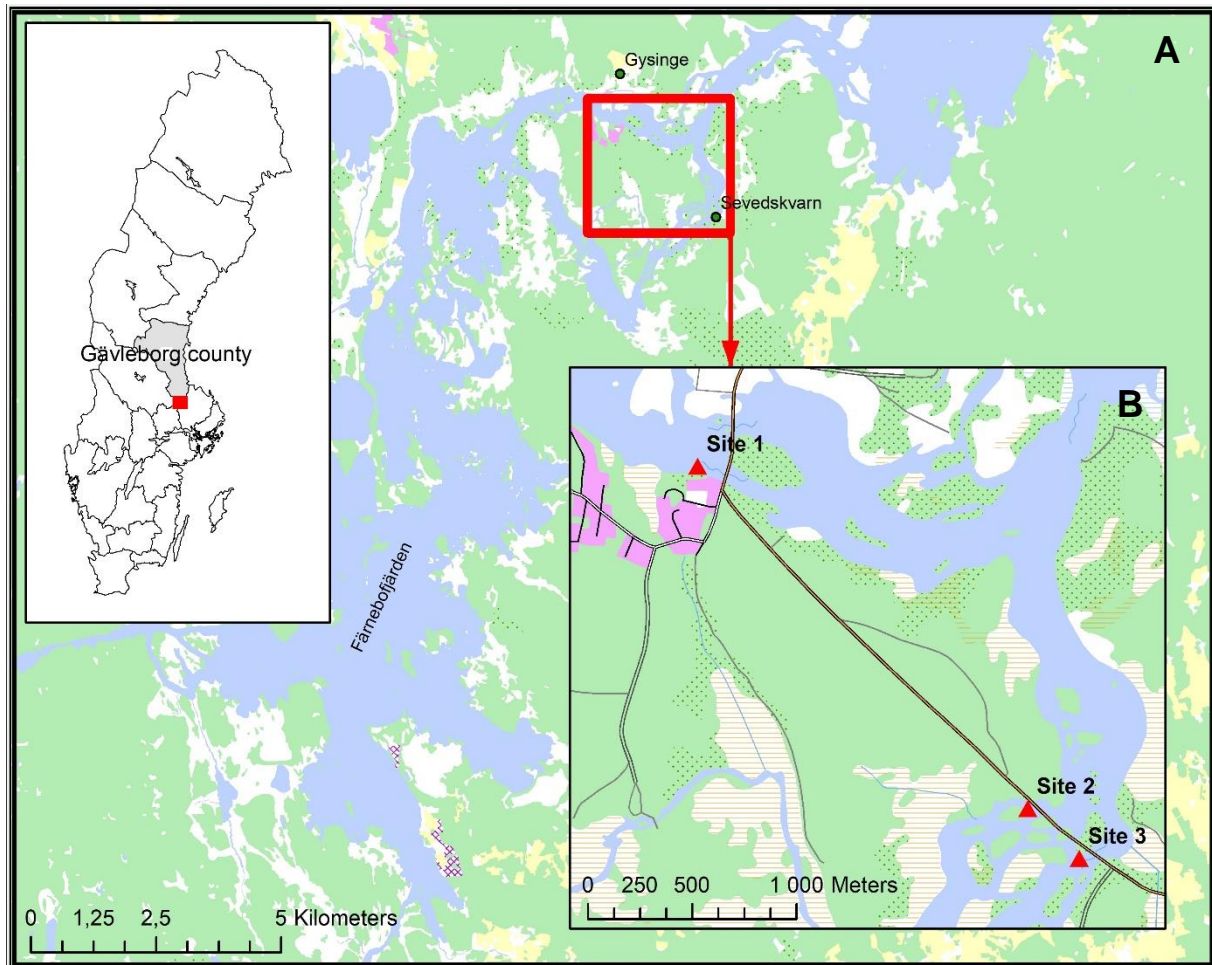
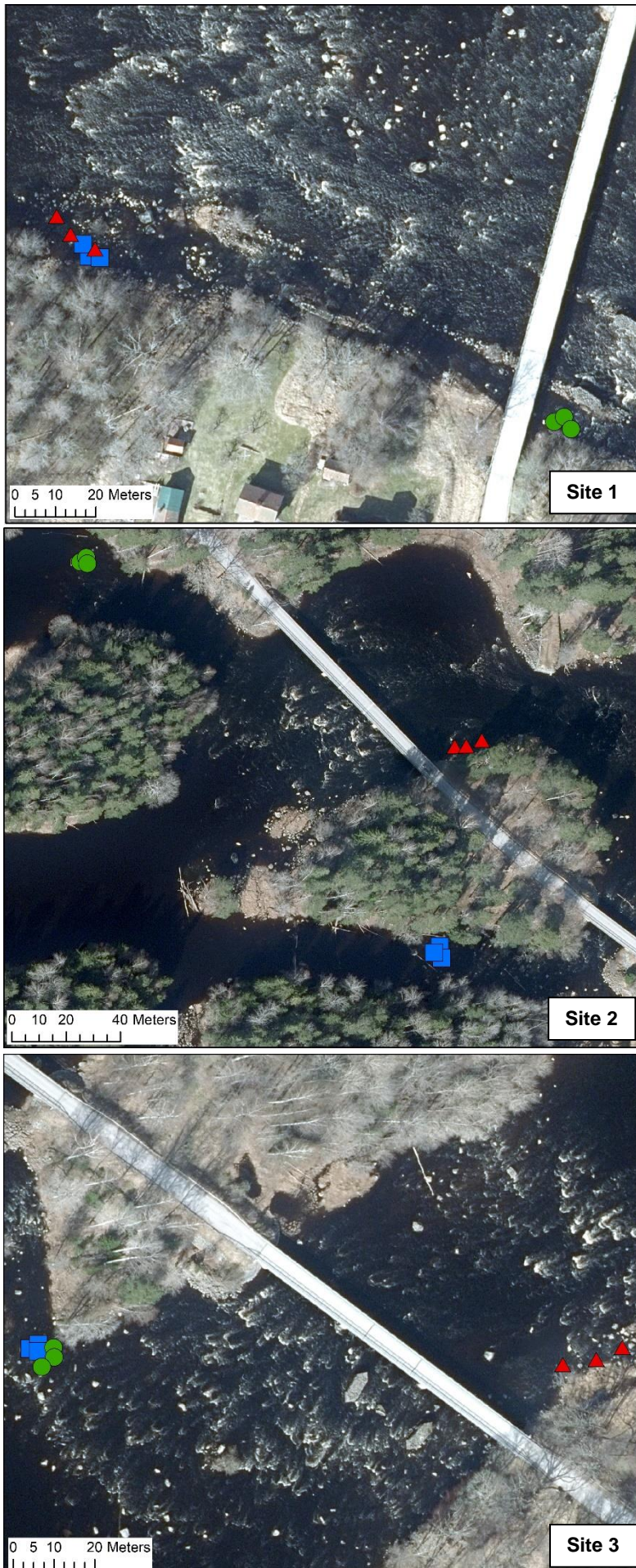


Figure 7. Map A shows the geographical location of the study area at Gysinge. The general locations of sites 1 – 3 are represented as red triangles in map B. North is up. Source: Lantmäteriet Topography 50. Gävleborg county marked in gray.

Site 1 (Fig. 7) was located in the river channel north of Mattön and is characterized by the 600 m long and 270 m wide rapid and close proximity to the upstream lake-like environment of Färnebofjärden. Restoration measures included channel reconfiguration using an excavator and manual addition of spawning substrate. Sites 2 and 3 (Fig. 7) were located in the southern channel which is characterized by its braided flow pattern around the many islands in the area. The rapids are generally shorter and narrower compared to site 1. The primary restoration measures implemented in sites 2 and 3 were addition of spawning substrate using a helicopter and channel reconfiguration using an excavator.

Figure 8. Spatial distribution of the MVWBs at the sampling locations of sites 1 to 3. Blue squares represent egg planting containers, red triangles non-restored sections and green circles restored sections. North is up. ©Lantmäteriet



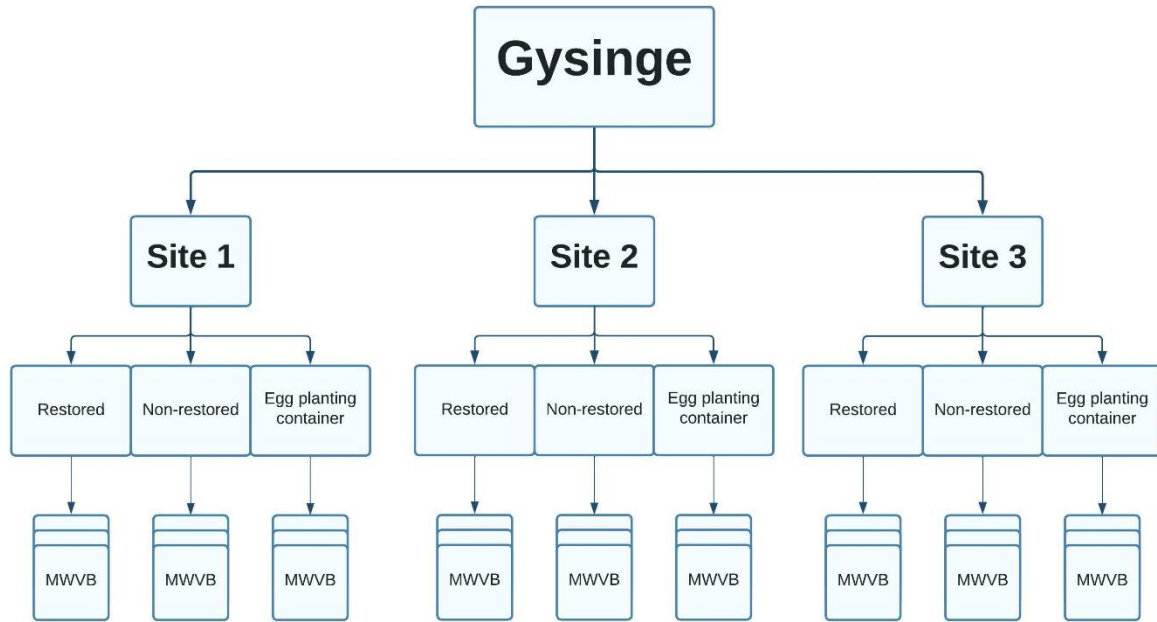


Figure 9. Conceptual hierarchical illustration of the study design. The different treatments restored, non-restored and egg planting container are nested within each site. Three MWVBs were used within each treatment at each site, resulting in a total of 27 MWVBs (9 restored, 9 non-restored and 9 egg planting containers). The MWVBs are the sampling units from which habitat variables and egg hatching rate were obtained.

3. Materials and methods

3.1 Modification of Whitlock-Vibert boxes

Whitlock-Vibert boxes are egg incubators (Whitlock 1995) which were modified so that they functioned both as egg incubators and units for sampling of hyporheic water (Fig. 10). 1 meter of silicone tubing (6 mm outer Ø, 4 mm inner Ø) was inserted into the lower compartment of each box. The tubing section inside of the MWVB was perforated with 6 holes (3 mm Ø). The end of the tubing was sealed with a clamp and attached to the wall to only allow flow through the perforations. The top end of the tubing was equipped with a quick connector and secured with a clamp to allow easy connection to a syringe during sampling. Half of the tubing was reinforced with a plastic sleeve to avoid obstruction of flow. Clean pebbles were added to the lower compartment of the MWVB to provide negative buoyancy without blocking the flow in the tubing. The modified Whitlock-Vibert boxes (MWVBs) were inspired from the “Egg-sandwich” designed by Pander *et al.* (2009). The method developed by Pander *et al.* (2009) was designed to collect data on hatching success and physicochemical water variables in order to assess stream substrate quality.

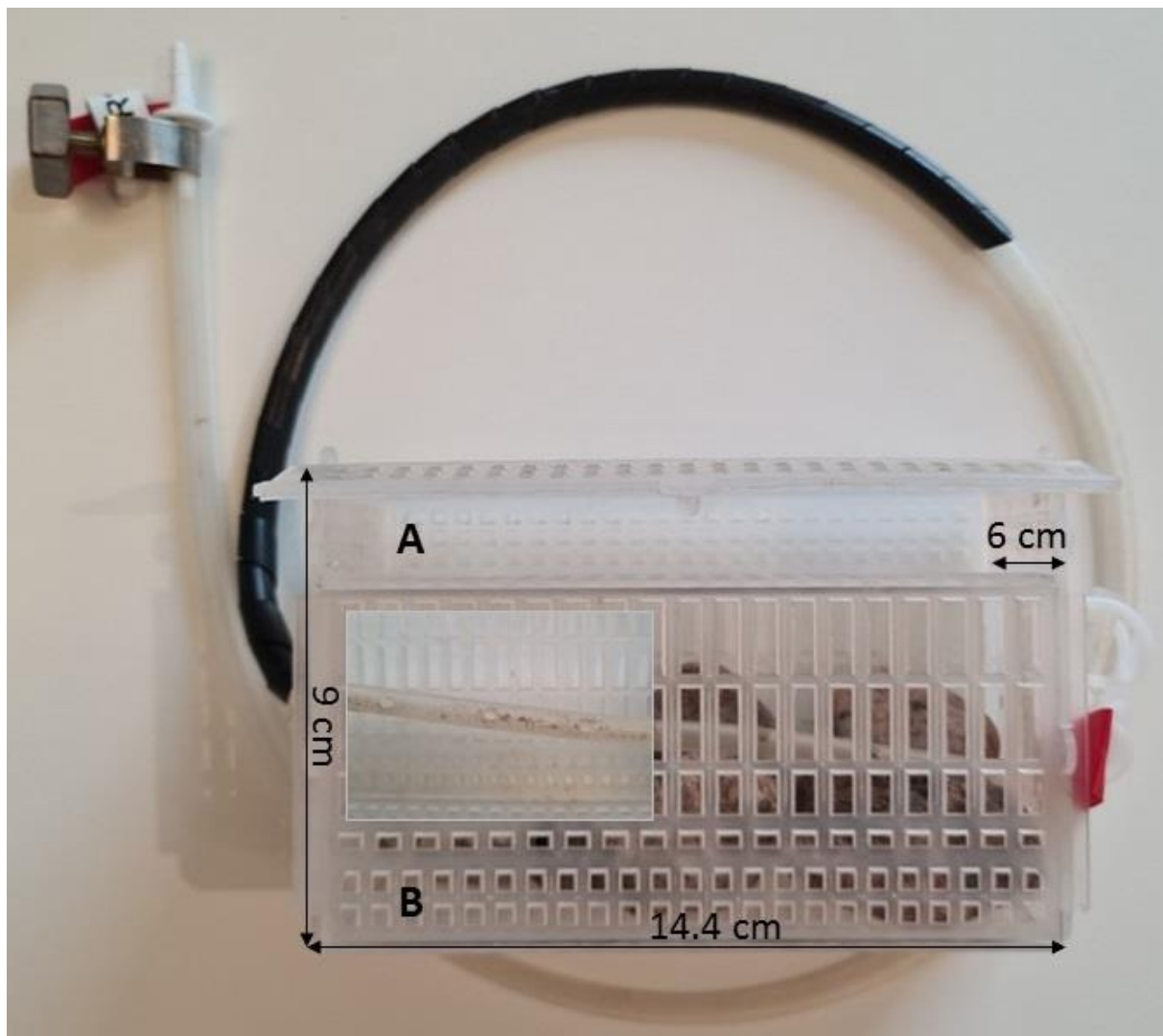


Figure 10. A modified Whitlock-Vibert box (MWVB). The upper compartment here with the lid open (A) is the incubator and the lower compartment (B) is where the newly hatched alevins can seek shelter.

3.2 Egg handling, excavation of redds and egg planting

Salmon eggs were collected from the hatchery at SLU Fisheries Research Station in Älvkarleby between 14-16th of March 2022. Excavation of redds and egg planting was carried out during the same period. The eggs were fertilized and incubated according to hatchery standard protocol and were well developed into the eyed egg-stage prior to collection. Barlaup & Moen (2001) recommends eggs in the eyed egg developmental stage for egg planting, as they are tolerant to handling (Barlaup & Moen 2001). Unfertilized and fungal infected eggs were removed at the hatchery prior to further handling and counting. 100 eggs were placed in the upper incubator compartment of each of the 27 MWVBs, amounting to a total of 2700 eggs. The MWVBs containing the eggs were then transported to the sampling sites in insulated Styrofoam boxes with ice to keep the eggs dark, cool and moisturized.

A total of 18 (9 restored and 9 non-restored) artificial redds designed according to Crisp & Carling (1989) were excavated at pre-determined restored and non-restored locations (Fig. 8) using shovels, picks and kicking-motions. The MWVBs were positioned in the deepest part (ca 20 cm) of the redds with the widest side turned against the current, and then covered with the excavated material. MWVBs were also placed in egg planting containers at pre-determined locations and covered with pebbles before being positioned on top of the riverbed (Fig. 11). The MWVBs were left undisturbed for two weeks before sampling started March 30th.



Figure 11. Preparation of an egg planting container. Three MVWBs are seen in the left picture. The two boxes which appear more orange are standard Whitlock-Vibert boxes filled with salmon eggs. In the middle picture the boxes are held in place and on the right picture pebbles are poured into the egg planting container to cover the boxes.

3.3 Sampling of hyporheic water

BD Plastipak syringes with a volume of 60 were used to extract hyporheic water samples. Sampling was performed at four occasions: March 28th, March 30th, April 6th and April 14th, 2022. The water samples were transported to the laboratory at Uppsala university to be analyzed the same day sampling was completed. The syringes and a short piece of tubing were attached to the tubing of the MWVB's using quick connectors. To not affect measurements, the volume of water retained in the tubing was removed before and between sampling. Two 60 ml syringes were filled from each MWVB. The samples to be used for measurements of dissolved oxygen and pH were sealed and placed in a dark cooler, awaiting transportation to the laboratory. Additionally, 15 ml of the water sample was filtered through a 0.2µm filter into a Falcontube which was then placed in a dark cooler with ice awaiting to be analyzed for ammonia in the lab. All MWVB's were sampled at each occasion, resulting in 27 samples. Additionally, surface water from the river channel was sampled at each site (1-3), to control for differentiation between the surface water, HZ and egg planting containers, resulting in 30 samples per occasion. The surface water samples will be referred to as control or C. However, two MWVB's (one restored at site 1, and one restored at site 2) were lost between egg planting and sampling, resulting in a total of 7 MWVB's at restored locations.

Water temperature and conductivity

Water temperature and conductivity were measured in-situ using a Hach HQ2200 multimeter. The probe was lowered into the syringe containing the extracted water sample. The probe was kept in river water and measurements were taken directly after extraction to not affect water temperature. Also, neoprene gloves were used during handling of the syringe and probe to avoid heat transfer. Water temperature is an important driver of salmon development (Jonsson & Jonsson 2011g), while together with conductivity it can also be used to determine the influence of groundwater on the HZ (Alexander & Caissie 2003, Arntzen *et al.* 2006).

Dissolved oxygen

In the laboratory, the samples were transferred into a glass bottle with an optic sensor placed in the lower part of the bottle. The bottle was overfilled from the bottom and up with the water sample amounting to twice the volume of the bottle to avoid contamination from atmospheric oxygen. Dissolved oxygen (mg/L) was then measured with a PreSens Fibox 3 Fiber Optic system.

pH

pH was measured at the laboratory with a Metrohm 826 pH Mobile Meter and a glass electrode. The water temperature was at room temperature (20°C) during measurements.

Ammonia

Ion chromatography was used to determine the ammonium (NH₄⁺) concentration of the samples. Determination was performed July 1st 2022 with a Metrohm ion chromatography system (883 Basic IC Plus and 919 Autosampler Plus). Aqueous ammonia is present as NH₄⁺ (ionized) and NH₃ (un-ionized). NH₃ is the form which is toxic to aquatic organisms (Finn 2007). The two forms are in equilibrium, depending on water temperature and pH (Emerson *et al.* 1975). Current methods are not able to obtain NH₄⁺ and NH₃ measurements separately, but it is possible to determine the NH₃ fraction if water temperature and pH are known for each sample. This can be achieved by using the formulas presented by Emerson *et al.* (1975);

First, the pKa constant is calculated using the equation where T = temperature in Kelvin:

$$pKa = 0.09018 + 2727.92/T$$

The NH₃ fraction (f) can then be calculated using the following equation:

$$f = 1/(10^{(pKa - pH)} + 1)$$

3.4 MWVB retrieval, hatching rate and accumulation of fine sediments

The MWVBs were retrieved on May 5th, 2022. To avoid loss of accumulated sediment during retrieval, the walls of the MWVB were covered. After retrieval they were placed into plastic buckets and opened up so that the number of unhatched eggs could be counted. Hatching success was determined as the ratio between unhatched eggs and the number of planted eggs for each MWVB.

The MWVB's in the plastic bucket were then thoroughly rinsed using Milli-Q water. The water and sediment which gathered in the plastic bucket were filtered through a 500 µm sieve to remove debris and sediment fractions larger than coarse sand. A sample was collected from the bucket containing the filtered solution with a sediment load < 500 µm. The samples were transported to the laboratory and placed in a muffle furnace to remove all liquid. They were then transferred to an oven at 300°C for 6 hours to remove all organic matter. This resulted in an inorganic powder which was mixed with Milli-Q water to create a solution that could be analyzed in a Mastersizer 3000 (Malvern Panalytical) particle analyzer. The result from the particle analysis represents the fraction of sediment particles smaller than 2 µm which had accumulated in the MVWBs between burial and retrieval.

3.5 Statistical methods

All data handling and statistical analysis were performed in RStudio 4.2.2 and SAS 9.4. Plots were produced using the packages *gg.plot2* (Wickham 2016), *viridis* (Garnier *et al.* 2021) and *multcompView* (Graves *et al.* 2019) in RStudio. The alpha level was set to 0.05. The data set which was used to test for differences in habitat variables and egg hatching rates between egg planting containers, restored and non-restored sections, is summarized in table 1. The abbreviations used for treatments are C (control), EC (egg planting container), R (restored) and NR (non-restored). C and EC represents the surface water environment, while R and NR represents the hyporheic environment. The output from the mixed effect models are compiled in Appendix A.

Interstitial water conditions

The function *proc mixed* in SAS was used to design mixed models to compare the conditions between treatments (control, restored, non-restored & egg planting container). Dissolved oxygen, water temperature, conductivity, pH and NH₃ were assigned as dependent variables in separate models with treatment and site as fixed effects. Since multiple measurements were made on the same units the samples were not independent of each other. Therefore, sampling time was added as a random factor using the REPEATED statement in the *proc mixed* function. The REPEATED statement calculates individual slopes for each observation. An interaction term between the fixed effects was also added to the models. All assumptions for mixed linear models were met except for NH₃ which had to be transformed using square root transformation. Note that the output from the models, least squares means, are not means of the sampled raw data, but modelled means which summarize the effects of fixed (treatment and site) and random effects (sampling time) on the dependent variable of the model. Least squares means were used to estimate between-group differences (treatments and sites).

Hatching rate and accumulation of fine sediment

RStudio and the functions *aov* and *Anova* from the *car* (Fox & Weisberg 2019) package was used to produce two-way ANOVAs to determine if treatment or site, or the interaction between treatment and site, had a significant effect on hatching success or accumulation of fine sediment, respectively. The *TukeyHSD* function was used to produce a Tukey Honest Significant Differences post hoc test. All assumptions for a two-way ANOVA were checked and met.

Table 1. The data set collected in the field containing 10 variables.

Variable	Type	Description
Site	Nominal	3 levels (1, 2 & 3)
Treatment	Nominal	4 levels (C, R, NR & EC)
Sample occasion	Ordinal	4 levels (T1, T2, T3 & T4)
Dissolved oxygen	Continuous	mg/L
Water temperature	Continuous	°C
Conductivity	Continuous	mS/m
pH	Continuous	
Ammonia (NH ₄ ⁺)	Continuous	µg/L
Accumulated fine sediment	Discrete	%
Egg hatching rate	Discrete	%

4. Results

Dissolved oxygen

Dissolved oxygen levels ranged between 6.35 mg/L and 8.26 mg/L (Fig. 12ab). The highest value was measured during the first sampling occasion at a restored location of site 1 and the lowest during the final sampling occasion at a restored section of site 3 (Fig. 12a). Mean dissolved oxygen levels were highest at site 1 for all treatments except NR, which was highest at site 2 (Fig. 12b). R had the highest mean dissolved oxygen levels out of all treatments (7.17, sd = 0.49). Dissolved oxygen in surface waters (treatment C) had a decreasing trend from the first sampling occasion (mean O₂ = 7.46 mg/L) to the third (mean O₂ = 6.8 mg/L), before increasing again at the fourth and final sampling occasion (mean O₂ = 7.07 mg/L) (Fig. 12a). In contrast, dissolved oxygen in all other treatments had a declining trajectory over the sampling period except for the spike in the restored treatment at the third sampling occasion (Fig. 12a). Treatment had no significant effect on the concentrations of dissolved oxygen. However, dissolved oxygen was significantly higher at site 1 (mean dissolved O₂ = 7.2 mg/L) compared to site 2 (mean dissolved O₂ = 7 mg/L) (estimate of between-group effects = 0.19, SE = 0.094, $P = 0.047$). A Chi-Square test of independence was performed to investigate if the frequency of dissolved oxygen levels below the lower critical limit of 7 mg/L differed between sites or treatments. The result from the Chi-Square revealed that the frequency did not differ between sites (X^2 (2, $n = 112$) = 1.40, $P = 0.5$) or treatments (X^2 (3, $n = 112$) = 1.32, $P = 0.72$). The frequency of dissolved oxygen levels below the critical threshold of 7 mg/L is summarized below in table 2.

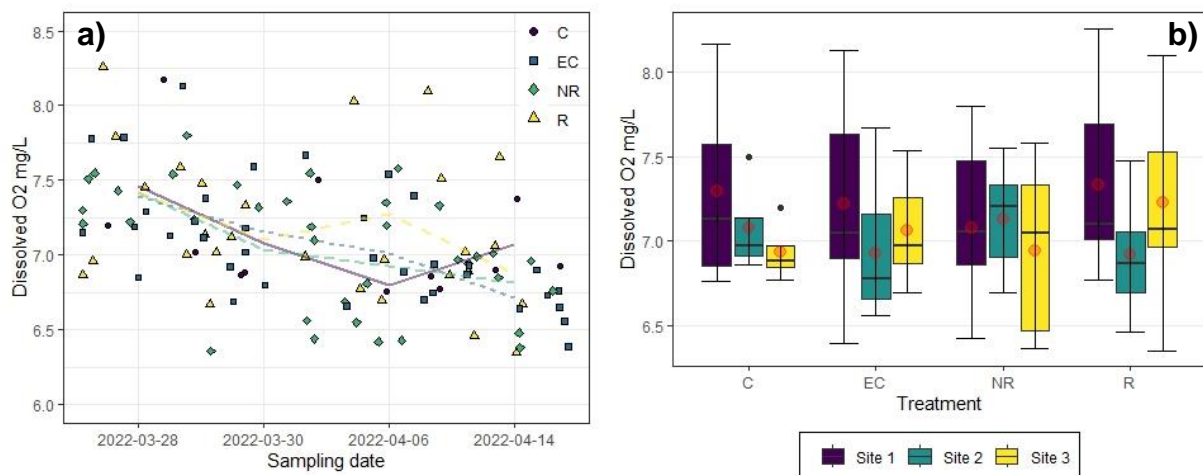


Figure 12. a) Dissolved oxygen concentration measured over all four sampling occasions. Vertical jitter was added for visual purposes. The dashed lines show the means of the treatments at each sampling occasion while the filled line represents the surface flow (treatment C). b) Box-and-whiskers plot representing dissolved oxygen in all combinations of treatment and site. Red circles illustrate the mean of each combination of treatment and site.

Table 2. Frequency table showing the number of observations where dissolved oxygen levels was below the lower critical limit of 7 mg/L oxygen.

	Site			Treatment			
	Site 1	Site 2	Site 3	C	EC	NR	R
Frequency	15	20	19	7	19	16	12

Water temperature

Water temperatures ranged from 1.7°C to 5°C during the sampling period. The coldest water temperature was in the surface water at site 3 during the second sampling occasion, and the warmest temperature was at a restored location of site 3 at the end of the sampling period (Fig. 13a). All treatments followed the same trend over the sampling period, with a decline in water temperature between the first two sampling occasions, and from there an increase (Fig. 13a). Overall, water temperature exhibited only minor variations between treatments, but in general, surface water temperatures (C mean water temperature = 2.78°C) was lower compared to the treatments (EC mean water temperature = 3.18°C, NR mean water temperature = 3.2°C, R mean water temperature = 3.1°C) (Fig. 13ab). Treatment and/or site had no statistically significant effect on water temperature.

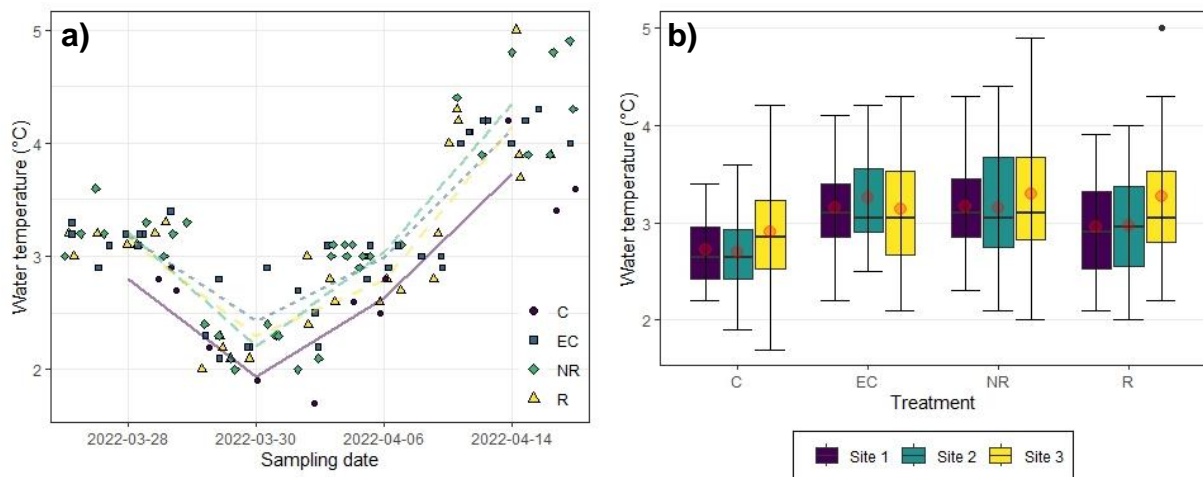


Figure 13. a) Water temperature measured over all four sampling occasions. Vertical jitter was added for visual purposes. The dashed lines show the means of the treatments at each sampling occasion while the filled line represents the surface flow (treatment C). b) Box-and-whiskers plot representing water temperature in all combinations of treatment and site. Red circles illustrate the mean of each combination of treatment and site.

pH

pH values ranged between 6.24-6.48 (Fig. 14b). The highest pH value was measured at a restored section of site 1 at the third sampling occasion, while the lowest value was measured at the final sampling occasion at a non-restored section of site 1 (Fig. 14a). pH levels in surface waters and all treatments increased from the first to the third sampling occasion and decreased from the third to the fourth and final occasion (Fig. 14a). pH in surface waters had the lowest initial mean pH value (C mean pH = 6.32) but had higher mean pH levels compared to all treatments at the third sampling occasion (C mean pH = 6.44, EC mean pH = 6.43, NR mean pH = 6.43, R mean pH = 6.42) (Fig. 14a). Treatment and/or site had no statistically significant effect on pH values.

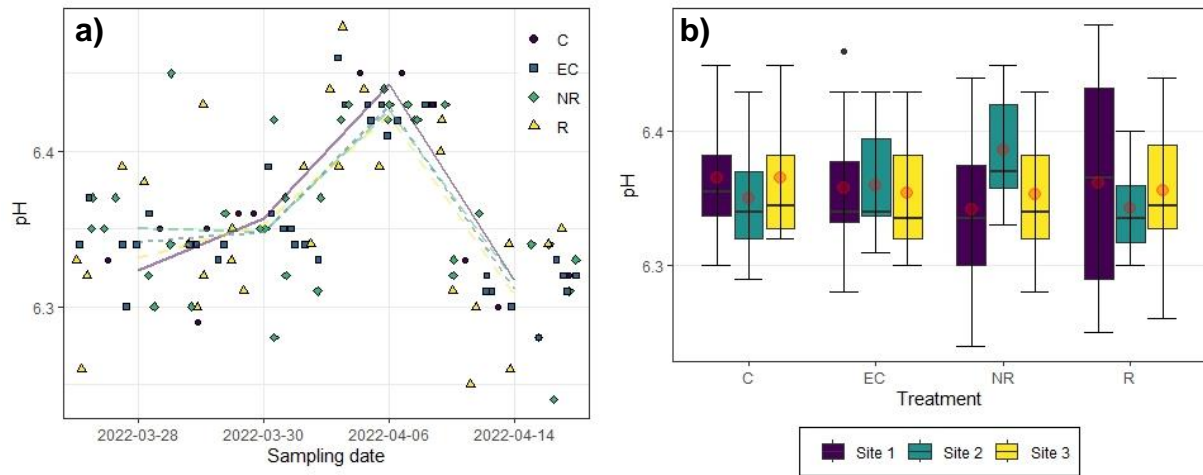


Figure 14. a) pH levels measured over all four sampling occasions. Vertical jitter was added for visual purposes. The dashed lines show the means of the treatments at each sampling occasion while the filled line represents the surface flow (treatment C). b) Box-and-whiskers plot representing pH levels in all combinations of treatment and site. Red circles illustrate the mean of each combination of treatment and site.

Conductivity

Conductivity had range of 41.2-44.9 mS/m and increased from its lowest value at the first sampling occasion to the maximum value during the peak at the third sampling occasion, before decreasing again at the final sampling occasion (Fig. 15a). Treatment had no statistically significant effect on conductivity and all treatments followed the same trajectory during the sampling period (Fig. 15.a). However, conductivity was statistically significantly higher at site 1 (mean conductivity 43.41 mS/m) compared to site 2 (mean conductivity = 42.7 mS/m) (estimate of between-group effects = 0.68, SE = 0.23, $P = 0.004$) and site 3 (mean conductivity = 42.62 mS/m) (estimate of between-group effects = 0.80, SE = 0.23, $P < 0.001$) (Fig. 15b).

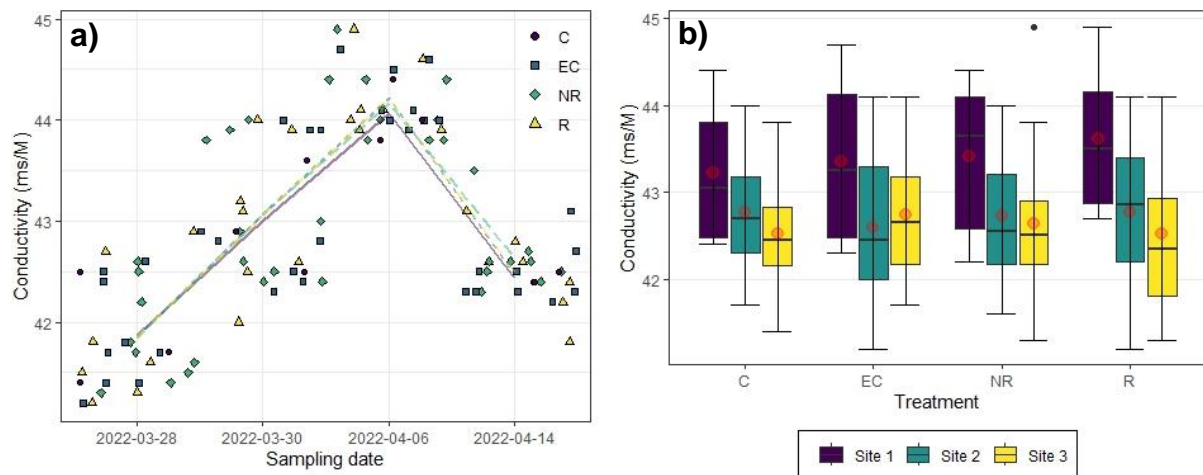


Figure 15. a) Conductivity measured over all four sampling occasions. Vertical jitter was added for visual purposes. The dashed lines show the means of the treatments at each sampling occasion while the filled line represents the surface flow (treatment C). b) Box-and-whiskers plot representing conductivity in all combinations of treatment and site. Red circles illustrate the mean of each combination of treatment and site.

NH_3

NH_3 concentrations were overall low and ranged from 0 to 0.0070 $\mu\text{g/L}$. The restored treatment showed the highest levels of variation ($\text{sd} = 0.0023$) (Fig. 16b). The initial NH_3 concentrations in the surface water were visibly separated from all treatments at the first sampling occasion, but they converged at the second sampling occasion (Fig. 16a). However, the trajectory of the restored treatment diverged from C and the other treatments at the fourth sampling occasion (Fig. 16a). The results from the mixed effect model showed that treatment and/or site had no statistically significant effect on NH_3 .

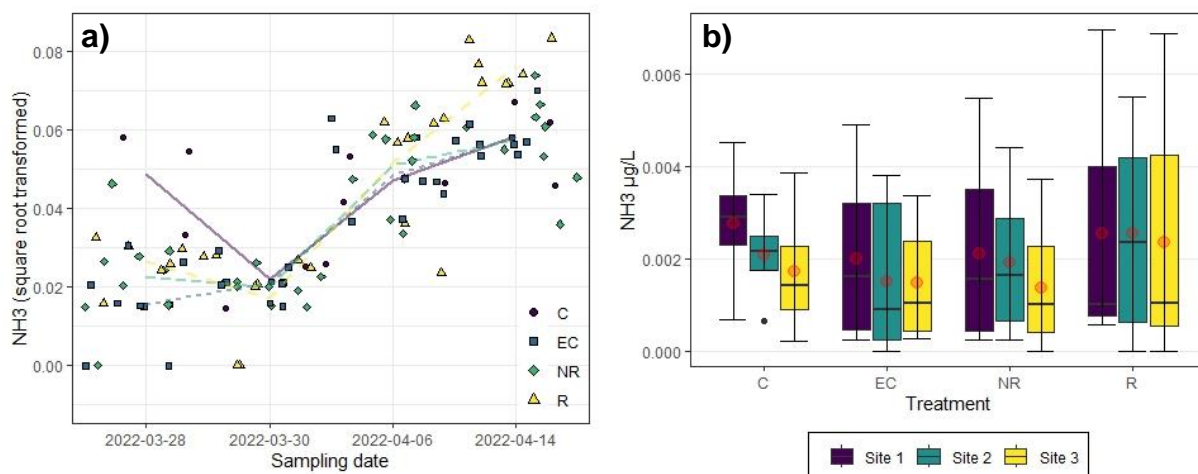


Figure 16. Note that data presented in figure a) is transformed while figure b) illustrates non-transformed data. a) NH_3 square root transformed over all four sampling occasions. Vertical jitter was added for visual purposes. The dashed lines show the means of the treatments at each sampling occasion while the filled line represents the surface flow (treatment C). b) Box-and-whiskers plot representing NH_3 in all combinations of treatment and site. Red circles illustrate the mean of each combination of treatment and site.

Hatching rate

Hatching rate ranged between 80 % and 100 %. The minimum value of hatching rate was observed in one egg planting container at site 3 and was the only observation of 80 % hatching rate, while there were 8 separate observations of 100 % hatching rate represented in all treatments distributed over sites 1 and 2. Treatment had no statistically significant effect on hatching rate (Table 2). However, site had a statistically significant effect on hatching rate ($F = 24.6$, $df = 2$, $P < 0.01$). A Tukey HSD post hoc test revealed that hatching rate at site 3 was significantly lower compared to site 1 ($P < 0.001$) and site 2 ($P < 0.001$) (Fig. 17). Hatching rates did not differ between site 1 and site 2 ($P=0.98$). At site 3, the mean hatching rate of the egg planting containers was 90.33 % ($N = 3$, $SD = 9.61$), followed by non-restored locations at 88.33 % ($N = 3$, $SD = 3.06$). The restored location at site 3 had the lowest mean hatching rate, 86% ($N = 3$, $SD = 2.65$) at that site. In contrast, the restored location of site 2 was the only combination of treatment and site which had 100% hatching rate (Fig. 17).

Table 3. Two-way ANOVA with independent variables and interaction term listed.

Effects	Sum Sq	df	F	P-value
<i>Treatment</i>	13.92	2	0.5	0.62
<i>Site</i>	686.76	2	24.6	>0.01
<i>Treatment:Site</i>	19.17	4	0.34	0.85
<i>Residuals</i>	223.33	16		

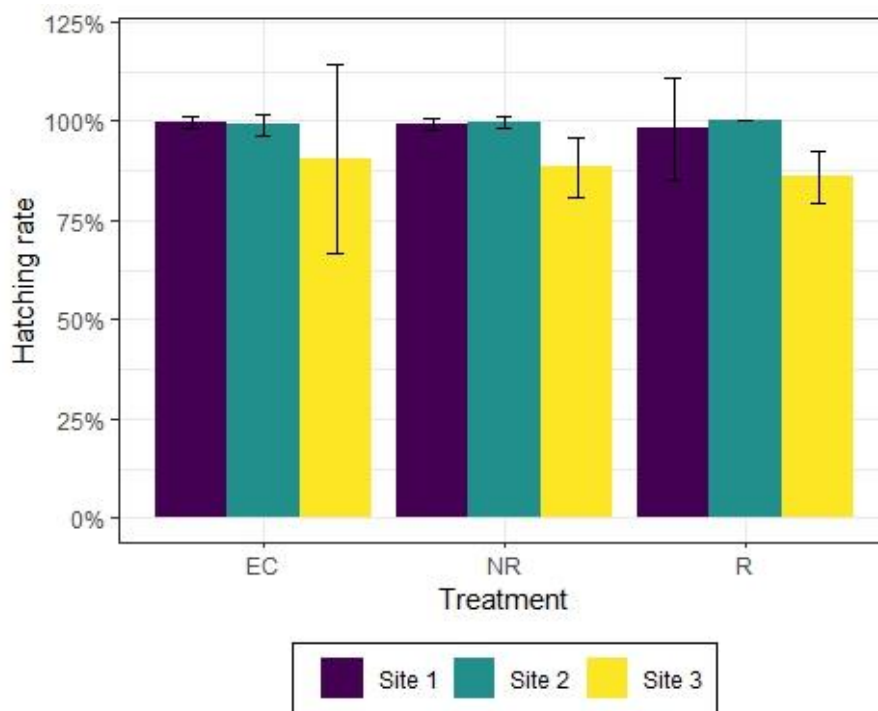


Figure 17. Bar plot representing mean egg hatching rate in all combinations of treatments and sites. Error bars show the 95% confidence interval and whiskers the standard error.

Accumulated clay particles

The fraction of sediment smaller than 2 μm which had accumulated in the MVWBs between burial and retrieval ranged between 1.32 % and 2.79 % (Fig. 18). The minimum and maximum values were observed in non-restored sections at sites 3 and 2 respectively. Treatment and/or site had no statistically significant effect on the accumulation of clay particles.

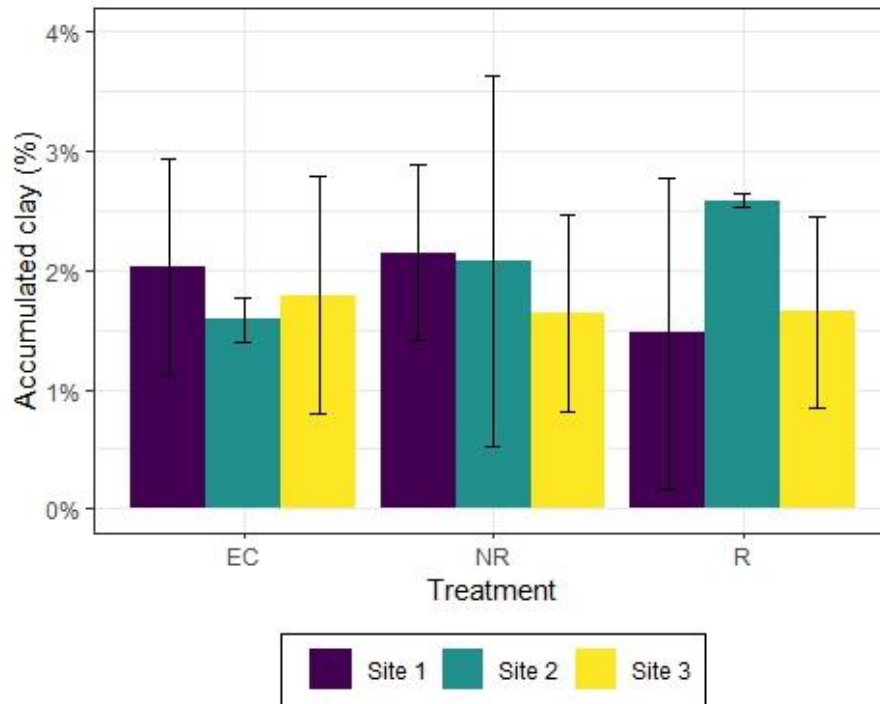


Figure 18. Bar plot representing the fraction of sediment smaller than 2 μm which had accumulated in the MVWBs between burial and retrieval. Error bars show the 95% confidence interval and whiskers the standard error.

Table 4. Mean values for each treatment (over all sites) and for each site (over all treatments).

	Treatment				Site		
	C	EC	NR	R	1	2	3
Dissolved oxygen (mg/L)							
n	12	36	36	28	36	36	40
mean	7.1	7.07	7.05	7.17	7.2	7	0.32
sd	0.41	0.4	0.41	0.49	0.49	7.06	0.42
Water temperature (°C)							
n	12	36	36	28	36	36	40
mean	2.78	3.18	3.2	3.1	3.06	3.1	3.2
sd	0.71	0.64	0.81	0.74	0.62	0.68	0.87
pH							
n	12	36	36	28	36	36	40
mean	6.36	6.36	6.36	6.35	6.35	6.36	6.36
sd	0.05	0.05	0.05	0.06	0.06	0.04	0.05
Conductivity (mS/m)							
n	12	36	36	28	36	36	40
mean	42.84	42.9	42.92	42.9	43.41	42.7	42.62
sd	0.92	0.99	0.97	1.03	0.88	0.92	0.94
NH3 (μg/L)							
n	12	36	36	28	36	36	40
mean	0.002	0.002	0.002	0.003	0.002	0.002	0.002
sd	0.001	0.001	0.002	0.002	0.002	0.002	0.002
Hatching rate (%)							
n	9	9	7	8	8	9	
mean	96.33	95.78	93.43	99.13	99.5	88.22	
sd	6.61	5.8	7.18	0.99	0.76	5.54	
Accumulation of clay particles (%)							
n	9	9	7	8	8	9	
mean	1.8	1.95	1.98	2.04	2.02	1.69	
sd	0.34	0.45	0.54	0.38	0.53	0.31	

5. Discussion

The results in this study indicates that hatching rate and habitat variables did not differ between restored and non-restored sites, but both hatching rate and habitat variables exhibited spatial variation. Overall, hatching rates were very high (range 80-100%, Fig. 17) and surpassed the expected hatching rates of 70 % in Smialek *et al.* (2021). This would indicate that both restored and non-restored sections of the Gysinge area may function as spawning grounds for salmon. It also seems that the egg planting containers, which are standing on the river bottom in the surface water, resembles the hyporheic environment of the study area more than the surface environment (Fig. 13 & Fig. 14).

Seen over the entire study period, the critical thresholds (as summarized by Smialek *et al.* 2021) of pH 4.5-9 and ammonia <0.004 mg/L were not breached in any of the treatments (Fig. 14 & Fig. 16). However, dissolved oxygen levels dropped below the lower critical limit of 7 mg/L dissolved oxygen during some of the sampling occasions, most notably during the final sampling occasion (Fig. 12a). Nonetheless, 6.35 mg/L dissolved oxygen which was the lowest measured value is still within a range which salmon may tolerate for shorter periods of time (Lavery & Cunjak 2019, Smialek *et al.* 2021). Salmon embryos have the highest oxygen demand just before hatching (Smialek *et al.* 2021), but the dissolved oxygen levels during hatching in this study are unknown since no measurements were made after April 14th. The individual MVWBs which had the lowest hatching rates (Kb3b3 80 %, R3b1 83 % & Nr3b2 85 %) were not affected by prolonged periods of dissolved oxygen levels below 7 mg/L (Appendices B & C). Only prolonged periods (>30 days) of oxygen deficiency have been shown to be harmful for salmon (Lavery & Cunjak 2019). Lavery & Cunjak (2019) used sensors over a period of two years to collect automated high frequency data of water temperature, dissolved oxygen and other abiotic variables which they then used to correlate embryo mortality and abiotic factors. They were able to relate prolonged periods (>30 days) of low concentrations of dissolved oxygen to increased embryo mortality, while shorter periods (2-5 days) had no effect on mortality rates (Lavery & Cunjak 2019).

Even if this present study didn't investigate the relationships between abiotic factors and egg hatching rate, Lavery & Cunjak (2019) showed that the ecology of salmon embryos is highly complex. Their model could only account for 38 % of the mortality variation in salmonid embryos, even though they used 22 carefully selected explanatory variables in their model (Lavery & Cunjak 2019). This indicates that it might be more difficult to identify ideal conditions for incubating salmonid eggs than initially hypothesized.

The apparent lack of response in physicochemical habitat variables and hatching rate following restoration in Gysinge could partly be explained by a biased site selection and habitat similarities between restored and non-restored sections. Particularly when considering the fact that both restored and non-restored sections are located in areas which previously have been assessed to be suitable for spawning (Hagelin *et al.* 2018). A study similar to this present study was performed by Sternecker *et al.* (2013b) who also used physicochemical habitat variables and hatching rate to evaluate restoration success. They were only able to identify higher hatching rates and more favorable conditions at restored sections when comparing observations pre- and post-restoration. However, Sternecker *et al.* (2013b) had a different study design which included before vs. after observations. This was not possible in this present study as the restoration efforts in Gysinge were made in 2016 and 2018. Also, the sampling frequency differed as Sternecker *et al.* (2013b) only collected data at two occasions post-restoration, 100

days apart. In contrast, data was collected at four occasions over a period of 18 days in this study. The temporal resolution in this present study is low overall, as only a small portion of the egg life stage was observed. A lack of response in the variables of interest in this study could partly be explained by the low sampling frequency (Rose *et al.* 2022), while the apparent response in physicochemical variables in the study by Sternecker *et al.* (2013b) could be an effect of natural variation in physicochemical variables between the sampling occasions. Since Sternecker *et al.* (2013b) performed sampling 100 days apart when autumn had turned to spring, one should expect seasonal variations in water temperature and flow conditions, which in turn also affect other physicochemical variables. Temporal trends in physicochemical habitat variables from Gysinge were easily observed, highlighting the necessity of frequent sampling to detect variation of measured variables. Especially in a heavily regulated river such as Nedre Dalälven where discharge may vary by the hour.

Additionally, the study by Sternecker *et al.* (2013b) was performed in a much smaller single-channel river with less spatial variation, compared to a large river such as lower Dalälven. The results from this present study did reveal spatial differences in hatching rates (Fig. 17) and habitat variables (Fig. 12ab & Fig. 15ab). The findings are in agreement with other studies which have shown that spatial factors exert considerable control on the functionality of spawning sites (Sternecker *et al.* 2013a, Sternecker *et al.* 2013b, Lavery & Cunjak 2019). According to Sternecker *et al.* (2013), this is because of the highly variable hyporheic conditions within rivers. In this present study, hatching rate was lower at site 3 compared to sites 1 and 2 (Fig. 17), but besides of conductivity, habitat variables at site 3 did not differ significantly from the other sites. Moreover, the results from the Chi-Square test revealed that the frequency of dissolved oxygen levels below the lower critical limit of 7 mg/L did not differ between sites. So even if hatching rate varied spatially, it seems that this variation cannot be explained by spatial variation of the measured habitat variables which are critical to the survival and development of salmon embryos.

The results from this study did not show significant gradients in physicochemical variables between the surface environment and the HZ. The similarity in observations between surface and hyporheic environments in Gysinge could indicate a well-defined HZ with high rates of hyporheic exchange flows. It may also indicate a short residence time in the HZ, which should be beneficial for salmon embryos, with a steady supply of oxygen rich water and removal of clay particles and waste products. Any distinct gradients in physicochemical variables of the HZ in Gysinge may be found deeper than 20 cm, which was the sample depth in this study, or at sites which were not sampled. Additionally, the conditions in the egg planting containers did not differ from the hyporheic environment and the thermal regime inside the egg planting containers resembled the thermal regime of the HZ more than the surface environment (Fig. 13a). Therefore, the method of using egg planting containers could possibly mimic the hyporheic environment in Gysinge where wild salmon would naturally deposit their eggs during spawning. The warmer hyporheic environment (Fig. 13a) is unlikely to be explained by upwelling of warmer groundwater since surface and hyporheic flow did not differ in conductivity and other measured parameters which are known to separate the hyporheic and surface environments. Inflow from the ice covered Färnebofjärden upstream of Gysinge is likely to have supplied the study area with cold water, as lake ice substantially cools near-surface water (Leppäranta *et al.* 2019). The low water temperatures observed at the second sampling occasion (Fig. 13a) coincides with the ice melt at Färnebofjärden which started around March 27th and the simultaneous peak in discharge during the same period (Fig. 6). The warmer

water observed in the hyporheic environment was likely due to hyporheic heat flux. During winter, riverbed heat flux is controlled by solar radiation and geothermal heating (Caissie 2006), which may heat interstitial water through conductive heat transfer when the water flows through the HZ (Evans *et al.* 1998, Caissie 2006). The above mentioned large-scale physical processes mainly impact water temperature and could explain why no other physicochemical variables differed between surface and hyporheic environments.

The levels of dissolved oxygen measured in both surface and hyporheic water were relatively low, with means close to the critical threshold (7 mg/L) for salmon embryos (Fig. 12ab). The low levels of dissolved oxygen might be explained by oxygen poor surface waters flowing to the Gysinge area from Färnebofjärden. The ice cover most likely inhibited atmospheric gas exchange (Terzhevik & Golosov 2012), and oxygen under the ice cover was at least partly depleted during microbial degradation of organic matter (Davis *et al.* 2020). However, re-oxygenation normally occurs around the time of ice breakup (Davis *et al.* 2020) and could explain why the levels of dissolved oxygen were not even lower. Additionally, the snow melt which was in full progress during the study period produced meltwater. Meltwater generally infiltrate the ground and affects the hydrologic gradient of the groundwater (Williams *et al.* 2015, Barnhart *et al.* 2016), and could force inflow of long residence groundwater low in oxygen. Meltwater normally produce an ionic pulse, if ions and solutes have accumulated in the snowpack over winter (Lee & Jung 2022). In this study, conductivity increased simultaneously as dissolved oxygen decreased during the third sampling occasion (Fig. 12 & Fig. 15a), which should be expected with higher ground- and meltwater input (Youngson *et al.* 2004, Lee & Jung 2022). Nevertheless, it is unclear if potential inputs of long residence groundwater or meltwater affected the results. Theoretically, pH values should have decreased with higher inputs of ground- and meltwater (Brunke & Gonser 1997, Lee & Jung 2022), but pH instead increased at the third sampling occasion (Fig. 14a). Additionally, NH₃ did increase (Fig. 16a) with increasing pH (Fig. 14a) and water temperature (Fig. 13a), just as theory suggests (Emerson *et al.* 1975), but NH₃ continued to increase (albeit at very low concentrations) during the fourth sampling occasion (Fig. 16a) when pH levels decreased again (Fig. 14a). The contradicting patterns in the results may be another consequence of insufficient spatiotemporal resolution in the sampling.

Furthermore, the accumulation of clay particles did not differ significantly between treatments or sites. Salmon is known to alter substrate composition during spawning, thus improving the conditions within the redd by removing the fine particles which might be harmful for incubating salmon eggs (Field-Dodgson 1987, Kondolf *et al.* 1993). Similar effects were observed by Sternecker *et al.* (2013a) when the construction of artificial redds caused a well-mixed zone without fines around the sampling units. It is likely that the construction of artificial redds in this present study had a similar effect and could be a reason why the accumulation of clay didn't differ between treatments or sites. Additionally, the incubating eggs were not likely to have been affected by accumulated clay particles, as the hatching rates were close to 100 % in most cases (Fig. 17). This is in agreement with the observations of accumulated clay in this study, which ranged between 1.3 to 2.8 % (Fig. 18). It is possible that the accumulation of clay particles would have differed if the MWVBs would have been buried earlier to be left undisturbed for a longer period. According to Sternecker *et al.* (2013a), the positive effects of redd construction diminished over time as fine particles began to accumulate after weeks to months. In contrast, Hauer *et al.* (2020) showed that artificially constructed spawning sites did not accumulate fine sediment over time but were rather reshaped or lost material due to scouring

and sediment transportation. In this study, two MWVBs were lost at locations where gravel had been added as a restoration measure. During the time between the burial of the MWVBs and the first sampling occasion there were two peaks in discharge (Fig. 6) which could have exposed and displaced the boxes due to scouring. The loss of the two sampling units in this study was not ideal. The locations where they were initially buried seems to be easily scoured and are therefore suboptimal spawning sites. The method of using MWVBs to assess the functionality of restored spawning grounds was successful, even if the two units were lost.

6. Conclusions

The results of this study indicate that the functionality of available spawning habitats in Gysinge is adequate in both restored and non-restored sections. Physicochemical habitat variables of importance for embryonic development and survival were within an acceptable range and hatching rates were high. Spatial variation in physicochemical habitat variables and hatching rate outweighed any differences between restored and non-restored sections, but the spatial variations are however negligible. The apparent lack of response to the restoration efforts in Gysinge is likely due to a combination of factors such as biased site selection, limited sampling period and a lack of comparable pre-restoration values. This highlights the need of defined restoration goals, a robust monitoring plan and criteria for evaluation of restoration success early in the planning stage of restoration projects. It is crucial to monitor ecosystem responses to restoration efforts in order to fully understand the outcome. When efforts are made to restore a river, it is important to do it thoroughly. There might be only one chance for it because of high costs in terms of administration and funding the actual restoration measures. One might argue that the investments in restoring nature could be at risk if restoration projects continue to provide inconclusive results of restoration success or base the evaluations on gut-feeling. Besides standardized procedures, practitioners in river restoration need a toolbox which enables them to monitor the habitat variables of interest. The Whitlock-Vibert box which was modified and used in this study is already a well-established piece of equipment in river management. Modifications to the Whitlock-Vibert box can produce a multi-purpose sampling unit which is both accessible and user-friendly. The unit should be developed further and combined with sensors that are able to produce long-term automated high frequency data. Assessment of restoration success should be more complete if data of habitat variables with high spatiotemporal resolution is included in monitoring. Monitoring of fish or other freshwater biota, which is the common practice today, is not sufficient on its own to fully assess restoration success, unless the only goal is to increase fish production. If biota is used as an ecological indicator it should be monitored long-term and combined with high frequency data of habitat variables.

Acknowledgements

Firstly, I would like to express my gratitude to my supervisor Sebastian Sobek who guided me throughout this experience. Thank you for your trust in me and for arranging meetings with other researchers to conceptualize the idea of this thesis. Also, thank you Olle Calles for your input and ideas, especially the simple but brilliant idea to use modified Whitlock-Vibert boxes. Karl Gullberg, thank you for your supervision and enthusiasm about the project. I also want to thank Linda Calamnius, Mattias Östling and everybody at the County Administrative Board of Gävleborg who helped me during my field work. Thank you Christoffer Bergvall for your patience and help in the lab. I am also grateful for the constructive feedback from my opponents, Sarah Shakil and Zakaria Hachicho.

I would like to thank my friends and family for your support. A special thanks to James for helping with the figure design, assistance in the field and for taking me out fishing when I needed a break. Lastly, thank you Hilja and Arvid for your endless love and support.

References

- Aas Ø, Klemetsen A, Einum S, Skurdal J, Skurdal J. 2010. *Atlantic Salmon Ecology*. John Wiley & Sons, Incorporated, Hoboken, United Kingdom.
- Acornley RM. 1999. Water temperatures within spawning beds in two chalk streams and implications for salmonid egg development. *Hydrological Processes* 13: 439–446.
- Albert JS, Destouni G, Duke-Sylvester SM, Magurran AE, Oberdorff T, Reis RE, Winemiller KO, Ripple WJ. 2021. Scientists' warning to humanity on the freshwater biodiversity crisis. *Ambio* 50: 85–94.
- Alexander MD, Caissie D. 2003. Variability and Comparison of Hyporheic Water Temperatures and Seepage Fluxes in a Small Atlantic Salmon Stream. *Groundwater* 41: 72–82.
- Allan JD. 2004. Landscapes and Riverscapes: The Influence of Land Use on Stream Ecosystems. *Annual Review of Ecology, Evolution, and Systematics* 35: 257–284.
- Allan JD, Castillo MM. 2007. The foundations of stream ecology. *Stream Ecology: Structure and function of running waters*, pp. 359–372. Springer Netherlands, Dordrecht.
- Altermatt F. 2013. Diversity in riverine metacommunities: a network perspective. *Aquatic Ecology* 47: 365–377.
- Andrén T, Björck S, Andrén E, Conley D, Zillén L, Anjar J. 2011. The Development of the Baltic Sea Basin During the Last 130 ka. In: Harff J, Björck S, Hoth P (ed.). *The Baltic Sea Basin*, pp. 75–97. Springer, Berlin, Heidelberg.
- Angus Webb J, Miller KA, King EL, de Little SC, Stewardson MJ, Zimmerman JKH, LeRoy Poff N. 2013. Squeezing the most out of existing literature: a systematic re-analysis of published evidence on ecological responses to altered flows. *Freshwater Biology* 58: 2439–2451.
- Arheimer B, Lindström G. 2015. Climate impact on floods: changes in high flows in Sweden in the past and the future (1911–2100). *Hydrology and Earth System Sciences* 19: 771–784.
- Armstrong JD, Kemp PS, Kennedy GJA, Ladle M, Milner NJ. 2003. Habitat requirements of Atlantic salmon and brown trout in rivers and streams. *Fisheries Research* 62: 143–170.
- Armstrong JD, Nislow KH. 2006. Critical habitat during the transition from maternal provisioning in freshwater fish, with emphasis on Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*). *Journal of Zoology* 269: 403–413.
- Arntzen EV, Geist DR, Dresel PE. 2006. Effects of fluctuating river flow on groundwater/surface water mixing in the hyporheic zone of a regulated, large cobble bed river. *River Research and Applications* 22: 937–946.
- Baran P, Delacoste M, Dauba F, Lascaux J-M, Belaud A, Lek S. 1995. Effects of reduced flow on brown trout (*Salmo trutta* L.) populations downstream dams in french pyrenees. *Regulated Rivers: Research & Management* 10: 347–361.
- Barbarossa V, Schmitt RJP, Huijbregts MAJ, Zarfl C, King H, Schipper AM. 2020. Impacts of current and future large dams on the geographic range connectivity of freshwater fish worldwide. *Proceedings of the National Academy of Sciences* 117: 3648–3655.
- Bardonnnet A, Baglinière J-L. 2000. Freshwater habitat of Atlantic salmon. 57: 10.
- Barlaup BT, Moen V. 2001. Planting of salmonid eggs for stock enhancement — a review of the most commonly used methods. *Nordic Journal of Freshwater Research*, 75: 7–19.
- Barlaup BT, Gabrielsen SE, Skoglund H, Wiers T. 2008. Addition of spawning gravel—a means to restore spawning habitat of atlantic salmon and Anadromous and resident brown trout in regulated rivers. *River Research and Applications* 24: 543–550.
- Barnhart TB, Molotch NP, Livneh B, Harpold AA, Knowles JF, Schneider D. 2016. Snowmelt rate dictates streamflow. *Geophysical Research Letters* 43: 8006–8016.

- Baxter CV, Fausch KD, Carl Saunders W. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. *Freshwater Biology* 50: 201–220.
- Baxter CV, Hauer FR. 2000. Geomorphology, hyporheic exchange, and selection of spawning habitat by bull trout (*Salvelinus confluentus*). *Canadian Journal of Fisheries and Aquatic Sciences* 57: 1470–1481.
- Baxter RM. 1977. Environmental Effects of Dams and Impoundments. *Annual Review of Ecology and Systematics* 8: 255–283.
- Baynes ERC, Attal M, Niedermann S, Kirstein LA, Dugmore AJ, Naylor M. 2015. Erosion during extreme flood events dominates Holocene canyon evolution in northeast Iceland. *Proceedings of the National Academy of Sciences* 112: 2355–2360.
- Becker CD, Neitzel DA. 1985. Assessment of intergravel conditions influencing egg and alevin survival during salmonid redd dewatering. *Environmental Biology of Fishes* 12: 33–46.
- Beechie T, Imaki H, Greene J, Wade A, Wu H, Pess G, Roni P, Kimball J, Stanford J, Kiffney P, Mantua N. 2013. Restoring Salmon Habitat for a Changing Climate. *River Research and Applications* 29: 939–960.
- Bellard C, Hugueny B. 2020. Importance of metapopulation dynamics to explain fish persistence in a river system. *Freshwater Biology* 65: 1858–1869.
- Belletti B, Garcia de Leaniz C, Jones J, Bizzi S, Börger L, Segura G, Castelletti A, van de Bund W, Aarestrup K, Barry J, Belka K, Berkhuisen A, Birnie-Gauvin K, Bussettini M, Carolli M, Consuegra S, Dopico E, Feierfeil T, Fernández S, Fernandez Garrido P, Garcia-Vazquez E, Garrido S, Giannico G, Gough P, Jepsen N, Jones PE, Kemp P, Kerr J, King J, Łapińska M, Lázaro G, Lucas MC, Marcello L, Martin P, McGinnity P, O’Hanley J, Olivo del Amo R, Parasiewicz P, Pusch M, Rincon G, Rodriguez C, Royte J, Schneider CT, Tummers JS, Vallesi S, Vowles A, Verspoor E, Wanningen H, Wantzen KM, Wildman L, Zalewski M. 2020. More than one million barriers fragment Europe’s rivers. *Nature* 588: 436–441.
- Biggs BJF, Nikora VI, Snelder TH. 2005. Linking scales of flow variability to lotic ecosystem structure and function. *River Research and Applications* 21: 283–298.
- Birk S, Chapman D, Carvalho L, Spears BM, Andersen HE, Argillier C, Auer S, Baattrup-Pedersen A, Banin L, Beklioğlu M, Bondar-Kunze E, Borja A, Branco P, Bucak T, Buijse AD, Cardoso AC, Couture R-M, Cremona F, de Zwart D, Feld CK, Ferreira MT, Feuchtmayr H, Gessner MO, Gieswein A, Globevnik L, Graeber D, Graf W, Gutiérrez-Cánovas C, Hanganu J, Işkın U, Järvinen M, Jeppesen E, Kotamäki N, Kuijper M, Lemm JU, Lu S, Solheim AL, Mischke U, Moe SJ, Nöges P, Nöges T, Ormerod SJ, Panagopoulos Y, Phillips G, Posthuma L, Pouso S, Prudhomme C, Rankinen K, Rasmussen JJ, Richardson J, Sagouis A, Santos JM, Schäfer RB, Schinegger R, Schmutz S, Schneider SC, Schülting L, Segurado P, Stefanidis K, Sures B, Thackeray SJ, Turunen J, Uyarra MC, Venohr M, von der Ohe PC, Willby N, Hering D. 2020. Impacts of multiple stressors on freshwater biota across spatial scales and ecosystems. *Nature Ecology & Evolution* 4: 1060–1068.
- Blöschl G, Hall J, Viglione A, Perdigão RAP, Parajka J, Merz B, Lun D, Arheimer B, Aronica GT, Bilibashi A, Boháč M, Bonacci O, Borga M, Čanjevac I, Castellarin A, Chirico GB, Claps P, Frolova N, Ganora D, Gorbachova L, Gül A, Hannaford J, Harrigan S, Kireeva M, Kiss A, Kjeldsen TR, Kohnová S, Koskela JJ, Ledvinka O, Macdonald N, Mavrova-Guirguinova M, Mediero L, Merz R, Molnar P, Montanari A, Murphy C, Osuch M, Ovcharuk V, Radevski I, Salinas JL, Sauquet E, Šraj M, Szolgay J, Volpi E, Wilson D, Zaimi K, Živković N. 2019. Changing climate both increases and decreases European river floods. *Nature* 573: 108–111.
- Boano F, Harvey JW, Marion A, Packman AI, Revelli R, Ridolfi L, Wörman A. 2014. Hyporheic flow and transport processes: Mechanisms, models, and biogeochemical implications. *Reviews of Geophysics* 52: 603–679.
- Boerger H. 1981. Species composition, abundance and emergence phenology of midges (Diptera: Chironomidae) in a brown-water stream of West-Central Alberta, Canada. *Hydrobiologia* 80: 7–30.
- Boulton AJ. 2007. Hyporheic rehabilitation in rivers: restoring vertical connectivity. *Freshwater Biology* 52: 632–650.
- Boulton AJ, Findlay S, Marmonier P, Stanley EH, Valett HM. 1998. The functional significance of the hyporheic zone in streams and rivers. *Annual Review of Ecology and Systematics* 29: 59–81.
- Boulton AJ, Hancock PJ, Boulton AJ, Hancock PJ. 2006. Rivers as groundwater-dependent ecosystems: a review of degrees of dependency, riverine processes and management implications. *Australian Journal of Botany* 54: 133–144.
- Boulton SJ, Stokes M, Mather AE. 2014. Transient fluvial incision as an indicator of active faulting and Plio-Quaternary uplift of the Moroccan High Atlas. *Tectonophysics* 633: 16–33.
- Bowerman T, Neilson BT, Budy P. 2014. Effects of fine sediment, hyporheic flow, and spawning site characteristics on survival and development of bull trout embryos. *Canadian Journal of Fisheries and Aquatic Sciences* 71: 1059–1071.
- Brunke M, Gonser T. 1997. The ecological significance of exchange processes between rivers and groundwater. *Freshwater Biology* 37: 1–33.
- Buttle JM, Beall FD, Webster KL, Hazlett PW, Creed IF, Semkin RG, Jeffries DS. 2018. Hydrologic response to and recovery from differing silvicultural systems in a deciduous forest landscape with seasonal snow cover. *Journal of Hydrology* 557: 805–825.
- Caissie D. 2006. The thermal regime of rivers: a review. *Freshwater Biology* 51: 1389–1406.
- Calles O, Nyberg L, Greenberg L. 2007. Temporal and spatial variation in quality of hyporheic water in one unregulated and two regulated boreal rivers. *River Research and Applications* 23: 829–842.

- Carignan R, Steedman RJ. 2000. Impacts of major watershed perturbations on aquatic ecosystems. *Canadian Journal of Fisheries and Aquatic Sciences* 57: 1–4.
- Carothers C, Black J, Langdon SJ, Donkersloot R, Ringer D, Coleman J, Gavenus ER, Justin W, Williams M, Christiansen F, Samuelson J, Stevens C, Woods B, Clark SJ, Clay PM, Mack L, Raymond-Yakoubian J, Sanders AA, Stevens BL, Whiting A. 2021. Indigenous peoples and salmon stewardship: a critical relationship. *Ecology and Society* 26: 16.
- Casas-Mulet R, Alfredsen K, Brabrand Å, Saltveit SJ. 2015. Survival of eggs of Atlantic salmon (*Salmo salar*) in a drawdown zone of a regulated river influenced by groundwater. *Hydrobiologia* 743: 269–284.
- Chapman DW. 1988. Critical Review of Variables Used to Define Effects of Fines in Redds of Large Salmonids. *Transactions of the American Fisheries Society* 117: 1–21.
- Chen W, Olden JD. 2017. Designing flows to resolve human and environmental water needs in a dam-regulated river. *Nature Communications* 8: 2158.
- Collins AL, Walling DE, McMellin GK, Zhang Y, Gray J, McGonigle D, Cherrington R. 2010. A preliminary investigation of the efficacy of riparian fencing schemes for reducing contributions from eroding channel banks to the siltation of salmonid spawning gravels across the south west UK. *Journal of Environmental Management* 91: 1341–1349.
- Collins AL, Williams LJ, Zhang YS, Marius M, Dungait JAJ, Smallman DJ, Dixon ER, Stringfellow A, Sear DA, Jones JI, Naden PS. 2014. Sources of sediment-bound organic matter infiltrating spawning gravels during the incubation and emergence life stages of salmonids. *Agriculture, Ecosystems & Environment* 196: 76–93.
- Collins SE, Matter SF, Buffam I, Flotemersch JE. 2018. A patchy continuum? Stream processes show varied responses to patch- and continuum-based analyses. *Ecosphere* 9: e02481.
- Côte J, Roussel J-M, Le Cam S, Bal G, Evanno G. 2012. Population differences in response to hypoxic stress in Atlantic salmon. *Journal of Evolutionary Biology* 25: 2596–2606.
- Crisp DT. 1988. Prediction, from temperature, of eyeing, hatching and ‘swim-up’ times for salmonid embryos. *Freshwater Biology* 19: 41–48.
- Crisp DT, Carling PA. 1989. Observations on siting, dimensions and structure of salmonid redds. *Journal of Fish Biology* 34: 119–134.
- Cummins KW. 1974. Structure and Function of Stream Ecosystems. *BioScience* 24: 631–641.
- Curry RA, Noakes DLG, Morgan GE. 1995. Groundwater and the incubation and emergence of brook trout (*Salvelinus fontinalis*). *Canadian Journal of Fisheries and Aquatic Sciences* 52: 1741–1749.
- Dale VH, Beyeler SC. 2001. Challenges in the development and use of ecological indicators. *Ecological Indicators* 1: 3–10.
- Dan Moore R, Spittlehouse DL, Story A. 2005. Riparian Microclimate and Stream Temperature Response to Forest Harvesting: A Review. *JAWRA Journal of the American Water Resources Association* 41: 813–834.
- Dannewitz J, Petersson E, Dahl J, Prestegard T, Löf A-C, Järvi T. 2004. Reproductive success of hatchery-produced and wild-born brown trout in an experimental stream. *Journal of Applied Ecology* 41: 355–364.
- Davis MN, McMahon TE, Cutting KA, Jaeger ME. 2020. Environmental and climatic factors affecting winter hypoxia in a freshwater lake: evidence for a hypoxia refuge and for re-oxygenation prior to spring ice loss. *Hydrobiologia* 847: 3983–3997.
- Décamps H, Naiman RJ, McClain ME. 2009. Riparian Zones. In: Likens GE (ed.). *Encyclopedia of Inland Waters*, pp. 396–403. Academic Press, Oxford.
- Deinet S, Scott-Gatty K, Rotton H, Twardek WM, Marconi V, McRae L, Baumgartner LJ, Brink K, Claussen JE, Cooke SJ, Darwall W, Eriksson BK, Garcia de Leaniz C, Hogan Z, Royte J, Silva LGM, Thieme ML, Tickner D, Waldman J, Wanningen H, Weyl OLF, Berkhuisen A. 2020. The Living Planet Index (LPI) for migratory freshwater fish: Technical Report. World Fish Migration Foundation, Groningen.
- DeVries P. 1997. Riverine salmonid egg burial depths: review of published data and implications for scour studies. *Canadian Journal of Fisheries and Aquatic Sciences* 54: 1685–1698.
- Diefenderfer HL, Steyer GD, Harwell MC, LoSchiavo AJ, Neckles HA, Burdick DM, Johnson GE, Buenau KE, Trujillo E, Callaway JC, Thom RM, Ganju NK, Twilley RR. 2020. Applying cumulative effects to strategically advance large-scale ecosystem restoration. *Frontiers in Ecology and the Environment*.
- Dieperink C, Bak BD, Pedersen L -F., Pedersen MI, Pedersen S. 2002. Predation on Atlantic salmon and sea trout during their first days as postsmolts. *Journal of Fish Biology* 61: 848–852.
- Diserud OH, Fiske P, Karlsson S, Glover KA, Næsje T, Aronsen T, Bakke G, Barlaup BT, Erkinaro J, Florø-Larsen B, Foldvik A, Heino M, Kanstad-Hanssen Ø, Lo H, Lund RA, Muladal R, Niemelä E, Økland F, Østborg GM, Otterå H, Skaala Ø, Skoglund H, Solberg I, Solberg MF, Sollien VP, Sægrov H, Urdal K, Wennevik V, Hindar K. 2022. Natural and anthropogenic drivers of escaped farmed salmon occurrence and introgression into wild Norwegian Atlantic salmon populations. *ICES Journal of Marine Science* 79: 1363–1379.
- Dudgeon D. 2019. Multiple threats imperil freshwater biodiversity in the Anthropocene. *Current Biology* 29: R960–R967.
- Dudgeon D, Arthington AH, Gessner MO, Kawabata Z-I, Knowler DJ, Lévêque C, Naiman RJ, Prieur-Richard A-H, Soto D, Stiassny MLJ, Sullivan CA. 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews* 81: 163–182.
- Ebersole JL, Liss WJ, Frissell CA. 2003. Thermal heterogeneity, stream channel morphology, and salmonid abundance in northeastern Oregon streams. *Canadian Journal of Fisheries and Aquatic Sciences* 60: 1266–1280.

- Eklöf K, Lidskog R, Bishop K. 2016. Managing Swedish forestry's impact on mercury in fish: Defining the impact and mitigation measures. *Ambio* 45: S163–S174.
- Elosegi A, Sabater S. 2013. Effects of hydromorphological impacts on river ecosystem functioning: a review and suggestions for assessing ecological impacts. *Hydrobiologia* 712: 129–143.
- Emerson K, Russo RC, Lund RE, Thurston RV. 1975. Aqueous Ammonia Equilibrium Calculations: Effect of pH and Temperature. *Journal of the Fisheries Research Board of Canada* 32: 2379–2383.
- Evans EC, McGregor GR, Petts GE. 1998. River energy budgets with special reference to river bed processes. *Hydrological Processes* 12: 575–595.
- Fagan WF. 2002. Connectivity, Fragmentation, and Extinction Risk in Dendritic Metapopulations. *Ecology* 83: 3243–3249.
- Falkenmark M. 2003. Water management and ecosystems: Living with change. GWP/TEC Background Papers No 9. Global Water Partnership, Stockholm.
- Feris K. P, Ramsey P, Frazar C, Rillig MC, Gannon J. E, Holben W. E. 2003. Structure and Seasonal Dynamics of Hyporheic Zone Microbial Communities in Free-Stone Rivers of the Western United States. *Microbial Ecology* 46: 200–215.
- Field-Dodgson MS. 1987. The effect of salmon redd excavation on stream substrate and benthic community of two salmon spawning streams in Canterbury, New Zealand. *Hydrobiologia* 154: 3–11.
- Findlay S. 1995. Importance of surface-subsurface exchange in stream ecosystems: The hyporheic zone. *Limnology and Oceanography* 40: 159–164.
- Findlay S. 2010. Stream microbial ecology. *Journal of the North American Benthological Society* 29: 170–181.
- Finn RN. 2007. The physiology and toxicology of salmonid eggs and larvae in relation to water quality criteria. *Aquatic Toxicology* 81: 337–354.
- Fleming IA. 1996. Reproductive strategies of Atlantic salmon: ecology and evolution. *Reviews in Fish Biology and Fisheries* 6: 379–416.
- Foote KJ, Biron PM, Grant JWA. 2020. Impact of in-stream restoration structures on salmonid abundance and biomass: an updated meta-analysis. *Canadian Journal of Fisheries and Aquatic Sciences* 77: 1574–1591.
- Forseth T, Barlaup BT, Finstad B, Fiske P, Gjøsæter H, Falkegård M, Hindar A, Mo TA, Rikardsen AH, Thorstad EB, Vøllestad LA, Wennevik V. 2017. The major threats to Atlantic salmon in Norway. *ICES Journal of Marine Science* 74: 1496–1513.
- Foster CN, Sato CF, Lindenmayer DB, Barton PS. 2016. Integrating theory into disturbance interaction experiments to better inform ecosystem management. *Global Change Biology* 22: 1325–1335.
- Fox J, Sanford W. 2019. An {R} Companion to Applied Regression, Third Edition. Thousand. Oaks CA: Sage.
- Friberg N, Bergfur J, Rasmussen J, Sandin L. 2013. Changing Northern catchments: Is altered hydrology, temperature or both going to shape future stream communities and ecosystem processes? *Hydrological Processes* 27: 734–740.
- Frissell CA, Liss WJ, Warren CE, Hurley MD. 1986. A hierarchical framework for stream habitat classification: Viewing streams in a watershed context. *Environmental Management* 10: 199–214.
- Galloway JN, Dentener FJ, Capone DG, Boyer EW, Howarth RW, Seitzinger SP, Asner GP, Cleveland CC, Green PA, Holland EA, Karl DM, Michaels AF, Porter JH, Townsend AR, Vörösmarty CJ. 2004. Nitrogen Cycles: Past, Present, and Future. *Biogeochemistry* 70: 153–226.
- Gann GD, McDonald T, Walder B, Aronson J, Nelson CR, Jonson J, Hallett JG, Eisenberg C, Guariguata MR, Liu J, Hua F, Echeverría C, Gonzales E, Shaw N, Decler K, Dixon KW. 2019. International principles and standards for the practice of ecological restoration. Second edition. *Restoration Ecology* 27: S1–S46.
- Garcia de Leaniz C, Fleming IA, Einum S, Verspoor E, Jordan WC, Consuegra S, Aubin-Horth N, Lajus D, Letcher BH, Youngson AF, Webb JH, Vøllestad LA, Villanueva B, Ferguson A, Quinn TP. 2007. A critical review of adaptive genetic variation in Atlantic salmon: implications for conservation. *Biological Reviews* 82: 173–211.
- Garnier S, Ross N, Rudis R, Camargo PA, Scialini M, Scherer C. 2021. viridis - Colorblind-Friendly Color Maps for R. R package version 0.6.2
- Geist J. 2010. Strategies for the conservation of endangered freshwater pearl mussels (*Margaritifera margaritifera* L.): a synthesis of Conservation Genetics and Ecology. *Hydrobiologia* 644: 69–88.
- Gooseff MN. 2010. Defining Hyporheic Zones – Advancing Our Conceptual and Operational Definitions of Where Stream Water and Groundwater Meet. *Geography Compass* 4: 945–955.
- Gooseff MN, Anderson JK, Wondzell SM, LaNier J, Haggerty R. 2006. A modelling study of hyporheic exchange pattern and the sequence, size, and spacing of stream bedforms in mountain stream networks, Oregon, USA. *Hydrological Processes* 20: 2443–2457.
- Göthe E, Degerman E, Sandin L, Segersten J, Tamario C, Mckie BG. 2019. Flow restoration and the impacts of multiple stressors on fish communities in regulated rivers. *Journal of Applied Ecology* 56: 1687–1702.
- Graf WL. 2008. Sources of Uncertainty in River Restoration Research. *River Restoration*, pp. 15–19. John Wiley & Sons, Ltd.
- Graves S, Piepho H, Dorai-Raj L. 2019. _multcompView: Visualizations of Paired Comparisons_. R. package version 0.1-8
- Greig SM, Sear DA, Carling PA. 2007. A review of factors influencing the availability of dissolved oxygen to incubating salmonid embryos. *Hydrological Processes* 21: 323–334.

- Greig SM, Sear DA, Smallman D, Carling PA. 2005. Impact of clay particles on the cutaneous exchange of oxygen across the chorion of Atlantic salmon eggs. *Journal of Fish Biology* 66: 1681–1691.
- Hagelin A, Calles O, Gullberg K. LIV – Laxfisk i nedre Dalälven. Rapport 2018:4. Länsstyrelsen Gävleborg.
- Hall CJ, Jordaan A, Frisk MG. 2011. The historic influence of dams on diadromous fish habitat with a focus on river herring and hydrologic longitudinal connectivity. *Landscape Ecology* 26: 95–107.
- Hanna DEL, Tomscha SA, Ouellet Dallaire C, Bennett EM. 2018. A review of riverine ecosystem service quantification: Research gaps and recommendations. *Journal of Applied Ecology* 55: 1299–1311.
- Hannah DM, Malcolm IA, Soulsby C, Youngson AF. 2004. Heat exchanges and temperatures within a salmon spawning stream in the Cairngorms, Scotland: seasonal and sub-seasonal dynamics. *River Research and Applications* 20: 635–652.
- Harding JS, Benfield EF, Bolstad PV, Helfman GS, Jones EBD. 1998. Stream biodiversity: The ghost of land use past. *Proceedings of the National Academy of Sciences* 95: 14843–14847.
- Harrison LR, Bray E, Overstreet B, Legleiter CJ, Brown RA, Merz JE, Bond RM, Nicol CL, Dunne T. 2019. Physical Controls on Salmon Redd Site Selection in Restored Reaches of a Regulated, Gravel-Bed River. *Water Resources Research* 55: 8942–8966.
- Harvey JW, Bencala KE. 1993. The Effect of streambed topography on surface-subsurface water exchange in mountain catchments. *Water Resources Research* 29: 89–98.
- Hauer C, Pulg U, Reisinger F, Flödl P. 2020. Evolution of artificial spawning sites for Atlantic salmon (*Salmo salar*) and sea trout (*Salmo trutta*): field studies and numerical modelling in Aurland, Norway. *Hydrobiologia* 847: 1139–1158.
- Havs- och vattenmyndigheten. 2022. Nationella planen (NAP). WWW document November 25th 2022: <https://www.havochvatten.se/arbete-i-vatten-och-energiproduktion/vattenkraftverk-och-dammar/nationella-planen-nap/regeringens-beslut-och-provningsgrupper.html>. Accessed 15 January 2023.
- Heaney S, Foy B, Kennedy G, Crozier W, Connor W. 2001. Impacts of agriculture on aquatic systems: Lessons learnt and new unknowns in Northern Ireland. *Marine and Freshwater Research* 52: 151–163.
- Heifetz J, Murphy ML, Koski KV. 1986. Effects of Logging on Winter Habitat of Juvenile Salmonids in Alaskan Streams. *North American Journal of Fisheries Management* 6: 52–58.
- Hesthagen T, Hansen LP. 1991. Estimates of the annual loss of Atlantic salmon, *Salmo salar* L., in Norway due to acidification. *Aquaculture Research* 22: 85–92.
- Hill AR, Labadia CF, Sanmugadas K. 1998. Hyporheic Zone Hydrology and Nitrogen Dynamics in Relation to the Streambed Topography of a N-Rich Stream. *Biogeochemistry* 42: 285–310.
- Hooke JM. 2007. Complexity, self-organisation and variation in behaviour in meandering rivers. *Geomorphology* 91: 236–258.
- Humphries P, Keckeis H, Finlayson B. 2014. The River Wave Concept: Integrating River Ecosystem Models. *BioScience* 64: 870–882.
- Hutchings JA, Ardren WR, Barlaup BT, Bergman E, Clarke KD, Greenberg LA, Lake C, Piironen J, Sirois P, Sundt-Hansen LE, Fraser DJ. 2019. Life-history variability and conservation status of landlocked Atlantic salmon: an overview. *Canadian Journal of Fisheries and Aquatic Sciences* 76: 1697–1708.
- Hvidsten NA. 1985. Mortality of pre-smolt Atlantic salmon, *Salmo salar* L., and brown trout, *Salmo trutta* L., caused by fluctuating water levels in the regulated River Nidelva, central Norway. *Journal of Fish Biology* 27: 711–718.
- Hynes HBN. 1975. The stream and its valley. *SIL Proceedings*, 1922-2010 19: 1–15.
- Hynes HBN. 1983. Groundwater and stream ecology. *Hydrobiologia* 100: 93–99.
- IPCC. 2021. Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change.
- Jackson MC, Loewen CJG, Vinebrooke RD, Chimimba CT. 2016. Net effects of multiple stressors in freshwater ecosystems: a meta-analysis. *Global Change Biology* 22: 180–189.
- Jacobson M, Charlson RJ, Rodhe H, Orians GH. 2000. *Earth System Science: From Biogeochemical Cycles to Global Changes*. Elsevier Science & Technology, London, UNITED KINGDOM.
- Jacobson P, Gårdmark A, Huss M. 2020. Population and size-specific distribution of Atlantic salmon *Salmo salar* in the Baltic Sea over five decades. *Journal of Fish Biology* 96: 408–417.
- Jähnig SC, Brabec K, Buffagni A, Erba S, Lorenz AW, Ofenböck T, Verdonschot PFM, Hering D. 2010. A comparative analysis of restoration measures and their effects on hydromorphology and benthic invertebrates in 26 central and southern European rivers. *Journal of Applied Ecology* 47: 671–680.
- Jähnig SC, Lorenz AW, Hering D, Antons C, Sundermann A, Jedicke E, Haase P. 2011. River restoration success: a question of perception. *Ecological Applications* 21: 2007–2015.
- Jensen AJ. 2003. Atlantic salmon (*Salmo salar*) in the regulated River Alta: effects of altered water temperature on parr growth. *River Research and Applications* 19: 733–747.
- Johnson JH. 2004. Comparative Survival and Growth of Atlantic Salmon from Egg Stocking and Fry Releases. *North American Journal of Fisheries Management* 24: 1409–1412.
- Jonsson B, Jonsson N. 2011a. Maturation and Spawning. In: Jonsson B, Jonsson N (ed.). *Ecology of Atlantic Salmon and Brown Trout: Habitat as a template for life histories*, pp. 327–414. Springer Netherlands, Dordrecht.
- Jonsson B, Jonsson N. 2011b. Species Diversity. In: Jonsson B, Jonsson N (ed.). *Ecology of Atlantic Salmon and Brown Trout: Habitat as a template for life histories*, pp. 23–66. Springer Netherlands, Dordrecht.

- Jonsson B, Jonsson N. 2011c. Recruitment, Mortality and Longevity. In: Jonsson B, Jonsson N (ed.). *Ecology of Atlantic Salmon and Brown Trout: Habitat as a template for life histories*, pp. 415–471. Springer Netherlands, Dordrecht.
- Jonsson B, Jonsson N. 2011d. Smolts and Smolting. In: Jonsson B, Jonsson N (ed.). *Ecology of Atlantic Salmon and Brown Trout: Habitat as a template for life histories*, pp. 211–245. Springer Netherlands, Dordrecht.
- Jonsson B, Jonsson N. 2011e. Climatic Effects on Atlantic Salmon and Brown Trout. In: Jonsson B, Jonsson N (ed.). *Ecology of Atlantic Salmon and Brown Trout: Habitat as a template for life histories*, pp. 473–515. Springer Netherlands, Dordrecht.
- Jonsson B, Jonsson N. 2011f. Population Enhancement and Population Restoration. In: Jonsson B, Jonsson N (ed.). *Ecology of Atlantic Salmon and Brown Trout: Habitat as a template for life histories*, pp. 567–632. Springer Netherlands, Dordrecht.
- Jonsson B, Jonsson N. 2011g. Development and Growth. In: Jonsson B, Jonsson N (ed.). *Ecology of Atlantic Salmon and Brown Trout: Habitat as a template for life histories*, pp. 137–209. Springer Netherlands, Dordrecht.
- Junk W, Bayley P, Sparks R. 1989. The Flood Pulse Concept in River-Floodplain Systems. 106:
- Juracek KE, Fitzpatrick FA. 2022. Geomorphic responses of fluvial systems to climate change: A habitat perspective. *River Research and Applications* 38: 757–775.
- Jutila E, Ahvonen A, Laamanen M, Koskiniemi J, Jutila E, A L. 1998. Adverse impact of forestry on fish and fisheries in stream environments of the Isojoki basin, western Finland. *Boreal Environment Research* 3:
- Kasahara T, Wondzell SM. 2003. Geomorphic controls on hyporheic exchange flow in mountain streams. *Water Resources Research* 39: SBH 3-1-SBH 3-14.
- Keinänen M, Käkälä R, Ritvanen T, Pönni J, Harjunpää H, Myllylä T, Vuorinen PJ. 2018. Fatty acid signatures connect thiamine deficiency with the diet of the Atlantic salmon (*Salmo salar*) feeding in the Baltic Sea. *Marine Biology* 165: 161.
- Koljonen S, Huusko A, Mäki-Petäys A, Louhi P, Muotka T. 2013. Assessing Habitat Suitability for Juvenile Atlantic Salmon in Relation to In-Stream Restoration and Discharge Variability. *Restoration Ecology* 21: 344–352.
- Kondolf GM, Sale MJ, Wolman MG. 1993. Modification of fluvial gravel size by spawning salmonids. *Water Resources Research* 29: 2265–2274.
- Kondolf GM, Wolman MG. 1993. The sizes of salmonid spawning gravels. *Water Resources Research* 29: 2275–2285.
- Koski P, Pakarinen M, Nakari T, Soivio A, Hartikainen K. 1999. Treatment with thiamine hydrochloride and astaxanthine for the prevention of yolk-sac mortality in Baltic salmon fry (M74 syndrome). *Diseases of Aquatic Organisms* 37: 209–220.
- Kurth A-M, Schirmer M. 2014. Thirty years of river restoration in Switzerland: implemented measures and lessons learned. *Environmental Earth Sciences* 72: 2065–2079.
- Larsson P, Backe C, Bremle G, Eklöv A, Okla L. 1996. Persistent pollutants in a salmon population (*Salmo salar*) of the southern Baltic Sea. 53: 8.
- Lavery JM, Cunjak RA. 2019. The influence of abiotic incubation conditions on the winter mortality of wild salmonid embryos. *Freshwater Biology* 64: 1098–1113.
- Lee J, Jung H. 2022. Understanding the relationship between meltwater discharge and solute concentration by modeling solute transport in a snowpack in snow-dominated regions – A review. *Polar Science* 31: 100782.
- Lenders HJR, Chamuleau TPM, Hendriks AJ, Lauwerier RCGM, Leuven RSEW, Verberk WCEP. 2016. Historical rise of waterpower initiated the collapse of salmon stocks. *Scientific Reports* 6: 29269.
- Lepori F, Palm D, Brännäs E, Malmqvist B. 2005. Does Restoration of Structural Heterogeneity in Streams Enhance Fish and Macroinvertebrate Diversity? *Ecological Applications* 15: 2060–2071.
- Leppäranta M, Lindgren E, Wen L, Kirillin G. 2019. Ice cover decay and heat balance in Lake Kilpisjärvi in Arctic tundra. *Journal of Limnology*.
- Liermann CR, Nilsson C, Robertson J, Ng RY. 2012. Implications of Dam Obstruction for Global Freshwater Fish Diversity. *BioScience* 62: 539–548.
- Ligon FK, Dietrich WE, Trush WJ. 1995. Downstream Ecological Effects of Dams. *BioScience* 45: 183–192.
- Likens GE. 2009. Inland Waters. In: Likens GE (ed.). *Encyclopedia of Inland Waters*, pp. 1–5. Academic Press, Oxford.
- Limburg KE. 2009. Aquatic Ecosystem Services. *Encyclopedia of Inland Waters*, pp. 25–30. Elsevier,
- Limburg KE, Waldman JR. 2009. Dramatic Declines in North Atlantic Diadromous Fishes. *BioScience* 59: 955–965.
- Löfgren S, Ring E, Brömssen C von, Sørensen R, Högbom L. 2009. Short-term Effects of Clear-cutting on the Water Chemistry of Two Boreal Streams in Northern Sweden: A Paired Catchment Study. *AMBIO: A Journal of the Human Environment* 38: 347–356.
- Lorenz AW, Feld CK. 2013. Upstream river morphology and riparian land use overrule local restoration effects on ecological status assessment. *Hydrobiologia* 704: 489–501.
- Louhi P, Mäki-Petäys A, Erkinaro J. 2008. Spawning habitat of Atlantic salmon and brown trout: general criteria and intragravel factors. *River Research and Applications* 24: 330–339.
- Louhi P, Vehanen T, Huusko A, Mäki-Petäys A, Muotka T. 2016. Long-term monitoring reveals the success of salmonid habitat restoration. *Canadian Journal of Fisheries and Aquatic Sciences*.
- Luckenbach T, Kilian M, Triebkorn R, Oberemm A. 2003. Assessment of the developmental success of brown trout (*Salmo trutta* f. *fario* L.) embryos in two differently polluted streams in Germany. *Hydrobiologia* 490: 53–62.

- Luckenbach T, Triebskorn R, Müller E, Oberemm A. 2001. Toxicity of waters from two streams to early life stages of brown trout (*Salmo trutta* f. *fario* L.), tested under semi-field conditions. *Chemosphere* 45: 571–579.
- Lund RA, Heggberget TG. 1992. Migration of Atlantic salmon, *Salmo salar* L., parr through a Norwegian fjord: potential infection path of *Gyrodactylus salaris*. *Aquaculture Research* 23: 367–372.
- Maasri A, Thorp JH, Kotlinski N, Kiesel J, Erdenee B, Jähnig SC. 2021. Variation in macroinvertebrate community structure of functional process zones along the river continuum: New elements for the interpretation of the river ecosystem synthesis. *River Research and Applications* 37: 665–674.
- Maazouzi C, Galassi D, Claret C, Cellot B, Fiers F, Martin D, Marmonier P, Dole-Olivier M-J. 2017. Do benthic invertebrates use hyporheic refuges during streambed drying? A manipulative field experiment in nested hyporheic flowpaths. *Ecohydrology* 10: e1865.
- MacCrimmon HR, Gots BL. 1979. World Distribution of Atlantic Salmon, *Salmo solar*. *Journal of the Fisheries Research Board of Canada* 36: 422–457.
- Macklin MG, Lewin J. 2015. The rivers of civilization. *Quaternary Science Reviews* 114: 228–244.
- Malcolm IA, Youngson AF, Soulsby C. 2003. Survival of salmonid eggs in a degraded gravel-bed stream: effects of groundwater–surface water interactions. *River Research and Applications* 19: 303–316.
- Manfrin A, Teurlinckx S, Lorenz AW, Haase P, Marttila M, Syrjänen JT, Thomas G, Stoll S. 2019. Effect of river restoration on life-history strategies in fish communities. *Science of The Total Environment* 663: 486–495.
- Manhard CV, Joyce JE, Gharrett AJ. 2017. Evolution of phenology in a salmonid population: a potential adaptive response to climate change. *Canadian Journal of Fisheries and Aquatic Sciences* 74: 1519–1527.
- Mäntyniemi S, Romakkaniemi A, Dannewitz J, Palm S, Pakarinen T, Pulkkinen H, Gårdmark A, Karlsson O. 2012. Both predation and feeding opportunities may explain changes in survival of Baltic salmon post-smolts. *ICES Journal of Marine Science* 69: 1574–1579.
- Marttila M, Louhi P, Huusko A, Mäki-Petäys A, Yrjänä T, Muotka T. 2016. Long-term performance of in-stream restoration measures in boreal streams. *Ecohydrology* 9: 280–289.
- McKinnell S. 1999. Spatial and temporal covariation in the recruitment and abundance of Atlantic salmon populations in the Baltic Sea. *ICES Journal of Marine Science* 56: 433–443.
- McLennan D, Auer SK, Anderson GJ, Reid TC, Bassar RD, Stewart DC, Cauwelier E, Sampayo J, McKelvey S, Nislow KH, Armstrong JD, Metcalfe NB. 2019. Simulating nutrient release from parental carcasses increases the growth, biomass and genetic diversity of juvenile Atlantic salmon. *Journal of Applied Ecology* 56: 1937–1947.
- Mellina E, Hinch SG. 2009. Influences of riparian logging and in-stream large wood removal on pool habitat and salmonid density and biomass: a meta-analysis. *Canadian Journal of Forest Research* 39: 1280–1301.
- Mittelbach GG, McGill BJ. 2019. Biodiversity and ecosystem functioning. In: Mittelbach GG, McGill BJ (ed.). *Community Ecology*, p. 0. Oxford University Press.
- Montgomery DR. 1999. Process Domains and the River Continuum1. *JAWRA Journal of the American Water Resources Association* 35: 397–410.
- Montgomery DR, Buffington JM. 1997. Channel-reach morphology in mountain drainage basins. *GSA Bulletin* 109: 596–611.
- Morandi B, Piégay H, Lamouroux N, Vaudor L. 2014. How is success or failure in river restoration projects evaluated? Feedback from French restoration projects. *Journal of Environmental Management* 137: 178–188.
- Mrozińska N, Glińska-Lewczuk K, Burandt P, Kobus S, Gotkiewicz W, Szymańska M, Bąkowska M, Obolowski K. 2018. Water Quality as an Indicator of Stream Restoration Effects—A Case Study of the Kwacza River Restoration Project. *Water* 10: 1249.
- Muhar S, Januschke K, Kail J, Poppe M, Schmutz S, Hering D, Buijse AD. 2016. Evaluating good-practice cases for river restoration across Europe: context, methodological framework, selected results and recommendations. *Hydrobiologia* 769: 3–19.
- Mulholland PJ, Hill WR. 1997. Seasonal patterns in streamwater nutrient and dissolved organic carbon concentrations: Separating catchment flow path and in-stream effects. *Water Resources Research* 33: 1297–1306.
- Myrvold KM, Mawle GW, Andersen O, Aas Ø. 2019. The Social, Economic and Cultural values of wild Atlantic salmon. A review of literature for the period 2009–2019 and an assessment of changes in values. NINA Report 1668. Norwegian Institute for Nature Research.
- Naiman RJ, Décamps H. 1997. The Ecology of Interfaces: Riparian Zones. *Annual Review of Ecology and Systematics* 28: 621–658.
- Newbold JD, Elwood JW, O'Neill RV, Winkle WV. 1981. Measuring Nutrient Spiralling in Streams. *Canadian Journal of Fisheries and Aquatic Sciences* 38: 860–863.
- Nieminen M, Sarkkola S, Laurén A. 2017. Impacts of forest harvesting on nutrient, sediment and dissolved organic carbon exports from drained peatlands: A literature review, synthesis and suggestions for the future. *Forest Ecology and Management* 392: 13–20.
- Nilsson C, Aradottir A, Hagen D, Halldórsson G, Høegh K, Mitchell R, Raulund-Rasmussen K, Svavarsdóttir K, Tolvanen A, Wilson S. 2016. Evaluating the process of ecological restoration. *Ecology and Society*.
- Nilsson C, Lepori F, Malmqvist B, Törnlund E, Hjerdt N, Helfield JM, Palm D, Östergren J, Jansson R, Brännäs E, Lundqvist H. 2005a. Forecasting Environmental Responses to Restoration of Rivers Used as Log Floatways: An Interdisciplinary Challenge. *Ecosystems* 8: 779–800.

- Nilsson C, Polvi LE, Gardeström J, Hasselquist EM, Lind L, Sarneel JM. 2015. Riparian and in-stream restoration of boreal streams and rivers: success or failure? *Ecohydrology* 8: 753–764.
- Nilsson C, Reidy CA, Dynesius M, Revenga C. 2005b. Fragmentation and Flow Regulation of the World's Large River Systems. *Science* 308: 405.
- Nyberg L, Calles O, Greenberg L. 2008. Impact of short-term regulation on hyporheic water quality in a boreal river. *River Research and Applications* 24: 407–419.
- O'Sullivan AM, Linnansaari T, Leavitt J, Samways KM, Kurylyk BL, Curry RA. The salmon-peloton: Hydraulic habitat shifts of adult Atlantic salmon (*Salmo salar*) due to behavioural thermoregulation. *River Research and Applications*.
- Palmer MA, Bernhardt E s., Allan JD, Lake P s., Alexander G, Brooks S, Carr J, Clayton S, Dahm CN, Follstad Shah J, Galat DL, Loss SG, Goodwin P, Hart D d., Hassett B, Jenkinson R, Kondolf G m., Lave R, Meyer J l., O'donnell T k., Pagano L, Sudduth E. 2005. Standards for ecologically successful river restoration. *Journal of Applied Ecology* 42: 208–217.
- Palmer MA, Allan JD, Meyer J, Bernhardt ES. 2007. River Restoration in the Twenty-First Century: Data and Experiential Knowledge to Inform Future Efforts. *Restoration Ecology* 15: 472–481.
- Palmer MA, Hondula KL, Koch BJ. 2014. Ecological Restoration of Streams and Rivers: Shifting Strategies and Shifting Goals. *Annual Review of Ecology, Evolution, and Systematics* 45: 247–269.
- Palmer MA, Reidy Liermann CA, Nilsson C, Flörke M, Alcamo J, Lake PS, Bond N. 2008. Climate change and the world's river basins: anticipating management options. *Frontiers in Ecology and the Environment* 6: 81–89.
- Palmer MA, Zedler JB, Falk DA. 2016. Ecological Theory and Restoration Ecology. In: Palmer MA, Zedler JB, Falk DA (ed.). *Foundations of Restoration Ecology*, pp. 3–26. Island Press/Center for Resource Economics, Washington, DC.
- Pander J, Geist J. 2013. Ecological indicators for stream restoration success. *Ecological Indicators* 30: 106–118.
- Pander J, Mueller M, Geist J. 2015. A Comparison of Four Stream Substratum Restoration Techniques Concerning Interstitial Conditions and Downstream Effects. *River Research and Applications* 31: 239–255.
- Pander J, Schnell J, Sternecker K, Geist J. 2009. The 'egg sandwich': a method for linking spatially resolved salmonid hatching rates with habitat variables in stream ecosystems. *Journal of Fish Biology* 74: 683–690.
- Parasiewicz P, Schmutz S, Moog O. 1998. The effect of managed hydropower peaking on the physical habitat, benthos and fish fauna in the River Bregenzerach in Austria. *Fisheries Management and Ecology* 5: 403–417.
- Peipoch M, Brauns M, Hauer FR, Weitere M, Valett HM. 2015. Ecological Simplification: Human Influences on Riverscape Complexity. *BioScience* 65: 1057–1065.
- Peterson BJ, Wollheim WM, Mulholland PJ, Webster JR, et al. 2001. Control of nitrogen export from watersheds by headwater streams. *Science* 292: 86–90.
- Petersson E, Jaurvi T, Steffner NG, Ragnarsson B. 1996. The effect of domestication on some life history traits of sea trout and Atlantic salmon. *Journal of Fish Biology* 48: 776–791.
- Petersson E, Rask J, Ragnarsson B, Karlsson L, Persson J. 2014. Effects of fin-clipping regarding adult return rates in hatchery-reared brown trout. *Aquaculture* 422–423: 249–252.
- Pistocchi A, Udias A, Grizzetti B, Gelati E, Koundouri P, Ludwig R, Papandreou A, Souliotis I. 2017. An integrated assessment framework for the analysis of multiple pressures in aquatic ecosystems and the appraisal of management options. *Science of The Total Environment* 575: 1477–1488.
- Poff N, Allan JD, Bain M, Karr J, Prestegard K, Richter B, Sparks R, Stromberg J. 1997. The Natural Flow Regime: A Paradigm for River Conservation and Restoration. *Bioscience* 47:
- Pulg U, Lennox RJ, Stranzl S, Espedal EO, Gabrielsen SE, Wiers T, Velle G, Hauer C, Dønnum BO, Barlaup BT. 2022. Long-term effects and cost-benefit analysis of eight spawning gravel augmentations for Atlantic salmon and Brown trout in Norway. *Hydrobiologia* 849: 485–507.
- Raymond PA, Hartmann J, Lauerwald R, Sobek S, McDonald C, Hoover M, Butman D, Striegl R, Mayorga E, Humborg C, Kortelainen P, Dürr H, Meybeck M, Ciais P, Guth P. 2013. Global carbon dioxide emissions from inland waters. *Nature* 503: 355–359.
- Rehbein JA, Watson JEM, Lane JL, Sonter LJ, Venter O, Atkinson SC, Allan JR. 2020. Renewable energy development threatens many globally important biodiversity areas. *Global Change Biology* 26: 3040–3051.
- Reid AJ, Carlson AK, Creed IF, Eliason EJ, Gell PA, Johnson PTJ, Kidd KA, MacCormack TJ, Olden JD, Ormerod SJ, Smol JP, Taylor WW, Tockner K, Vermaire JC, Dudgeon D, Cooke SJ. 2019. Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biological Reviews* 94: 849–873.
- Robinson M, Cognard-Plancq A-L, Cosandey C, David J, Durand P, Führer H-W, Hall R, Hendriques MO, Marc V, McCarthy R, McDonnell M, Martin C, Nisbet T, O'Dea P, Rodgers M, Zollner A. 2003. Studies of the impact of forests on peak flows and baseflows: a European perspective. *Forest Ecology and Management* 186: 85–97.
- Roni P. 2019. Does River Restoration Increase Fish Abundance and Survival or Concentrate Fish? The Effects of Project Scale, Location, and Fish Life History. *Fisheries* 44: 7–19.
- Roni P, Hanson K, Beechie T. 2008. Global Review of the Physical and Biological Effectiveness of Stream Habitat Rehabilitation Techniques. *North American Journal of Fisheries Management* 28: 856–890.
- Ros T. 1981. Salmonids in the lake Vänern area. *Ecological Bulletins* 21–31.

- Rose KC, McBride CG, Moriarty VW. 2022. Creating and Managing Data From High-Frequency Environmental Sensors. In: Mehner T, Tockner K (ed.). *Encyclopedia of Inland Waters (Second Edition)*, pp. 549–569. Elsevier, Oxford.
- Rothschild RE. 2019. *Poisonous Skies: Acid Rain and the Globalization of Pollution*. University of Chicago Press, Chicago, UNITED STATES.
- Rubin Z, Kondolf GM, Rios-Touma B. 2017. Evaluating Stream Restoration Projects: What Do We Learn from Monitoring? *Water* 9: 174.
- Rydén J. 2022. Statistical analysis of possible trends for extreme floods in northern Sweden. *River Research and Applications* 38: 1041–1050.
- Salmenkova EA. 2017. Mechanisms of homing in salmonids. *Biology Bulletin Reviews* 7: 287–298.
- Saltveit SJ, Halleraker J h., Arnekleiv J v., Harby A. 2001. Field experiments on stranding in juvenile atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) during rapid flow decreases caused by hydropeaking. *Regulated Rivers: Research & Management* 17: 609–622.
- Saltveit SJ, Brabrand Å. 2013. Incubation, hatching and survival of eggs of Atlantic salmon (*Salmo salar*) in spawning redds influenced by groundwater. *Limnologica* 43: 325–331.
- Samways KM, Blair TJ, Charest MA, Cunjak RA. 2017. Effects of spawning Atlantic salmon (*Salmo salar*) on total lipid content and fatty acid composition of river food webs. *Ecosphere* 8: e01818.
- Schmera D, Árva D, Boda P, Bódis E, Bolgovics Á, Borics G, Csercsa A, Deák C, Krasznai EÁ, Lukács BA, Mauchart P, Móra A, Sály P, Specziár A, Süveges K, Szivák I, Takács P, Tóth M, Várbíró G, Vojtkó AE, Erős T. 2018. Does isolation influence the relative role of environmental and dispersal-related processes in stream networks? An empirical test of the network position hypothesis using multiple taxa. *Freshwater Biology* 63: 74–85.
- Schwenk J, Lanzoni S, Foufoula-Georgiou E. 2015. The life of a meander bend: Connecting shape and dynamics via analysis of a numerical model. *Journal of Geophysical Research: Earth Surface* 120: 690–710.
- Scruton DA., Anderson T c., King L w. 1998. Pamehac Brook: a case study of the restoration of a Newfoundland, Canada, river impacted by flow diversion for pulpwood transportation. *Aquatic Conservation: Marine and Freshwater Ecosystems* 8: 145–157.
- Sear DA, Pattison I, Collins AL, Smallman DJ, Jones JJ, Naden PS. 2017. The magnitude and significance of sediment oxygen demand in gravel spawning beds for the incubation of salmonid embryos. *River Research and Applications* 33: 1642–1654.
- Shore M, Murphy S, Mellander P-E, Shortle G, Melland AR, Crockford L, O’Flaherty V, Williams L, Morgan G, Jordan P. 2017. Influence of stormflow and baseflow phosphorus pressures on stream ecology in agricultural catchments. *Science of The Total Environment* 590–591: 469–483.
- Smialek N, Pander J, Geist J. 2021. Environmental threats and conservation implications for Atlantic salmon and brown trout during their critical freshwater phases of spawning, egg development and juvenile emergence. *Fisheries Management and Ecology* 28: 437–467.
- Snelder TH, Biggs BJF. 2002. Multiscale River Environment Classification for Water Resources Management I. *JAWRA Journal of the American Water Resources Association* 38: 1225–1239.
- Soulsby C, Malcolm I a., Youngson A f. 2001. Hydrochemistry of the hyporheic zone in salmon spawning gravels: a preliminary assessment in a degraded agricultural stream. *Regulated Rivers: Research & Management* 17: 651–665.
- Stanford JA, Ward JV. 1988. The hyporheic habitat of river ecosystems. *Nature* 335: 64–66.
- Sternecker K, Cowley DE, Geist J. 2013a. Factors influencing the success of salmonid egg development in river substratum. *Ecology of Freshwater Fish* 22: 322–333.
- Sternecker K, Wild R, Geist J. 2013b. Effects of substratum restoration on salmonid habitat quality in a subalpine stream. *Environmental Biology of Fishes* 96: 1341–1351.
- Storey RG, Howard KWF, Williams DD. 2003. Factors controlling riffle-scale hyporheic exchange flows and their seasonal changes in a gaining stream: A three-dimensional groundwater flow model. *Water Resources Research*.
- Strayer DL, Dudgeon D. 2010. Freshwater biodiversity conservation: recent progress and future challenges. *Journal of the North American Benthological Society* 29: 344–358.
- Strömberg B. 1981. Calving Bays, Striae and Moraines at Gysinge-Hedesunda, Central Sweden. *Geografiska Annaler Series A, Physical Geography* 63: 149–154.
- Suddaby R. 2010. Editor’s Comments: Construct Clarity in Theories of Management and Organization. *The Academy of Management Review* 35: 346–357.
- Suuronen P, Lehtonen E. 2012. The role of salmonids in the diet of grey and ringed seals in the Bothnian Bay, northern Baltic Sea. *Fisheries Research* 125–126: 283–288.
- Syrjänen JT, Ruokonen TJ, Ketola T, Valkeajärvi P. 2015. The relationship between stocking eggs in boreal spawning rivers and the abundance of brown trout parr. *ICES Journal of Marine Science* 72: 1389–1398.
- Tautz AF, Groot C. 1975. Spawning Behavior of Chum Salmon (*Oncorhynchus keta*) and Rainbow Trout (*Salmo gairdneri*). *Journal of the Fisheries Research Board of Canada* 32: 633–642.
- Taylor EB. 1991. A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. *Aquaculture* 98: 185–207.

- Terzhevik A, Golosov S. 2012. Dissolved Oxygen in Ice-Covered Lakes. In: Bengtsson L, Herschy RW, Fairbridge RW (ed.). *Encyclopedia of Lakes and Reservoirs*, pp. 220–222. Springer Netherlands, Dordrecht.
- Thibodeaux LJ, Boyle JD. 1987. Bedform-generated convective transport in bottom sediment. *Nature* 325: 341–343.
- Thorp JH, Thoms MC, Delong MD. 2006. The riverine ecosystem synthesis: biocomplexity in river networks across space and time. *River Research and Applications* 22: 123–147.
- Thurston RV, Russo RC. 1983. Acute Toxicity of Ammonia to Rainbow Trout. *Transactions of the American Fisheries Society* 112: 696–704.
- Tonkin JD. 2022. Climate Change and Extreme Events in Shaping River Ecosystems. In: Mehner T, Tockner K (ed.). *Encyclopedia of Inland Waters (Second Edition)*, pp. 653–664. Elsevier, Oxford.
- Tonteri A, Titov S, Veselov A, Zubchenko A, Koskinen MT, Lesbarrères D, Kaluzhin S, Bakhmet I, Lumme J, Primmer CR. 2005. Phylogeography of anadromous and non-anadromous Atlantic salmon (*Salmo salar*) from northern Europe. *Annales Zoologici Fennici* 42: 1–22.
- Van Looy K, Tonkin JD, Flourey M, Leigh C, Soininen J, Larsen S, Heino J, LeRoy Poff N, Delong M, Jähnig SC, Datry T, Bonada N, Rosebery J, Jamoneau A, Ormerod SJ, Collier KJ, Wolter C. 2019. The three Rs of river ecosystem resilience: Resources, recruitment, and refugia. *River Research and Applications* 35: 107–120.
- Vannote RL, Minshall GW, Cummins KW, Sedell JR, Cushing CE. 1980. The River Continuum Concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37: 130–137.
- Vedel NE, Korsgaard B, Jensen FB. 1998. Isolated and combined exposure to ammonia and nitrite in rainbow trout (*Oncorhynchus mykiss*): effects on electrolyte status, blood respiratory properties and brain glutamine/glutamate concentrations. *Aquatic Toxicology* 41: 325–342.
- Vollset KW, Skoglund H, Wiers T, Barlaup BT. 2016. Effects of hydropeaking on the spawning behaviour of Atlantic salmon *Salmo salar* and brown trout *Salmo trutta*. *Journal of Fish Biology* 88: 2236–2250.
- Vörösmarty CJ, McIntyre PB, Gessner MO, Dudgeon D, Prusevich A, Green P, Glidden S, Bunn SE, Sullivan CA, Liermann CR, Davies PM. 2010. Global threats to human water security and river biodiversity. *Nature* 467: 555–561.
- Vosyliënė MZ, Kazlauskienė N. 2004. Comparative Studies of Sublethal Effects of Ammonia on Rainbow Trout (*Oncorhynchus Mykiss*) at Different Stages of its Development. *Acta Zoologica Lituanica* 14: 13–18.
- Ward JV. 1989. The Four-Dimensional Nature of Lotic Ecosystems. *Journal of the North American Benthological Society* 8: 2–8.
- Ward JV, Tockner K, Arscott DB, Claret C. 2002. Riverine landscape diversity. *Freshwater Biology* 47: 517–539.
- Weber C, Peter A. 2011. Success or Failure? Do Indicator Selection and Reference Setting Influence River Rehabilitation Outcome? *North American Journal of Fisheries Management* 31: 535–547.
- Wheaton JM, Pasternack GB, Merz JE. 2004. Spawning habitat rehabilitation -I. Conceptual approach and methods. *International Journal of River Basin Management* 2: 3–20.
- White DS. 1993. Perspectives on Defining and Delineating Hyporheic Zones. *Journal of the North American Benthological Society* 12: 61–69.
- Whitehead PG, Wilby RL, Battarbee RW, Kernan M, Wade AJ. 2009. A review of the potential impacts of climate change on surface water quality. *Hydrological Sciences Journal* 54: 101–123.
- Whitlock D. 1995. *The Whitlock Vibert Box Handbook*. 3rd printing. Federation of Fly Fishers. Livingston.
- Wickham H. 2016. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York.
- Williams GP, Wolman MG. 1984. Downstream effects of dams on alluvial rivers. Professional Paper.
- Williams MW, Hood E, Molotch NP, Caine N, Cowie R, Liu F. 2015. The ‘teflon basin’ myth: hydrology and hydrochemistry of a seasonally snow-covered catchment. *Plant Ecology & Diversity* 8: 639–661.
- Willson MF, Halupka KC. 1995. Anadromous Fish as Keystone Species in Vertebrate Communities. *Conservation Biology* 9: 489–497.
- Winemiller KO, Flecker AS, Hoeinghaus DJ. 2010. Patch dynamics and environmental heterogeneity in lotic ecosystems. *Journal of the North American Benthological Society* 29: 84–99.
- Wohl E, Angermeier PL, Bledsoe B, Kondolf GM, MacDonnell L, Merritt DM, Palmer MA, Poff NL, Tarboton D. 2005. River restoration. *Water Resources Research*.
- Wohl E, Lane SN, Wilcox AC. 2015. The science and practice of river restoration. *Water Resources Research* 51: 5974–5997.
- Wondzell SM. 2011. The role of the hyporheic zone across stream networks. *Hydrological Processes* 25: 3525–3532.
- Wooltorton S, Poelina A, Collard L. 2022. River relationships: For the love of rivers. *River Research and Applications* 38: 393–403.
- Wright KK. 2021. Assessing stream restoration and the influence of scale, variable choice, and comparison sites. *Ecosphere* 12: e03440.
- Young PS, Cech JJ, Thompson LC. 2011. Hydropower-related pulsed-flow impacts on stream fishes: a brief review, conceptual model, knowledge gaps, and research needs. *Reviews in Fish Biology and Fisheries* 21: 713–731.
- Youngson AF, Malcolm IA, Thorley JL, Bacon PJ, Soulsby C. 2004. Long-residence groundwater effects on incubating salmonid eggs: low hyporheic oxygen impairs embryo development. *Canadian Journal of Fisheries and Aquatic Sciences* 61: 2278–2287.
- Zarnetske JP, Haggerty R, Wondzell SM, Baker MA. 2011. Dynamics of nitrate production and removal as a function of residence time in the hyporheic zone. *Journal of Geophysical Research: Biogeosciences*.
- Zimmer MA, Lautz LK. 2015. Pre- and postrestoration assessment of stream water–groundwater interactions: effects on hydrological and chemical heterogeneity in the hyporheic zone. *Freshwater Science* 34: 287–300.

Appendices

Appendix A Output from the mixed effect models

Dependent variable	Effect	Comparisons		Estimate	DF	P-value
Dissolved oxygen	Treatment	EC	NR	0.023	98	0.784
	Treatment	EC	R	-0.090	98	0.331
	Treatment	EC	C	-0.021	98	0.864
	Treatment	NR	R	-0.113	98	0.221
	Treatment	NR	C	-0.044	98	0.716
	Treatment	R	C	0.069	98	0.582
	Site	2	3	-0.024	98	0.798
	Site	2	1	-0.190	98	0.047
	Site	3	1	-0.166	98	0.075
Water temperature	Treatment	EC	NR	-0.027	98	0.891
	Treatment	EC	R	0.108	98	0.617
	Treatment	EC	C	0.404	98	0.153
	Treatment	NR	R	0.135	98	0.530
	Treatment	NR	C	0.431	98	0.128
	Treatment	R	C	0.296	98	0.313
	Site	2	3	-0.138	98	0.521
	Site	2	1	0.029	98	0.895
	Site	3	1	0.167	98	0.438
pH	Treatment	EC	NR	-0.002	98	0.784
	Treatment	EC	R	0.003	98	0.757
	Treatment	EC	C	-0.004	98	0.718
	Treatment	NR	R	0.005	98	0.574
	Treatment	NR	C	-0.002	98	0.866
	Treatment	R	C	-0.007	98	0.566
	Site	2	3	0.004	98	0.695
	Site	2	1	0.000	98	0.964
	Site	3	1	-0.004	98	0.662
Conductivity	Treatment	EC	NR	-0.026	98	0.902
	Treatment	EC	R	-0.071	98	0.755
	Treatment	EC	C	0.057	98	0.847
	Treatment	NR	R	-0.045	98	0.843
	Treatment	NR	C	0.083	98	0.780
	Treatment	R	C	0.128	98	0.679
	Site	2	3	0.114	98	0.619
	Site	2	1	-0.684	98	0.004
	Site	3	1	-0.798	98	0.001
NH3 (sqrt transformed)	Treatment	EC	NR	-0.002	98	0.747
	Treatment	EC	R	-0.010	98	0.233
	Treatment	EC	C	-0.011	98	0.308
	Treatment	NR	R	-0.007	98	0.370
	Treatment	NR	C	-0.008	98	0.427
	Treatment	R	C	-0.001	98	0.916
	Site	2	3	0.003	98	0.694
	Site	2	1	-0.005	98	0.583
	Site	3	1	-0.008	98	0.341

Appendix B

Physicochemical variables full data set

ID	Site	Treatment	Sampling date	Dissolved oxygen (mg/L)	Conductivity (mS/s)	Water temperature (°C)	pH	NH4+ (µg/L)
r1b2	1	R	2022-03-28	8.26	42.7	3.2	6.34	4
r1b3	1	R	2022-03-28	7.79	42.9	3.2	6.3	5
nr1b1	1	NR	2022-03-28	7.54	42.2	3.3	6.3	4
nr1b2	1	NR	2022-03-28	7.51	42.6	3.2	6.32	1
nr1b3	1	NR	2022-03-28	7.8	42.5	3	6.3	2
kb1b1	1	EC	2022-03-28	8.13	42.5	2.9	6.34	1
kb1b2	1	EC	2022-03-28	7.79	42.4	3.2	6.36	1
kb1b3	1	EC	2022-03-28	7.78	42.6	3.2	6.34	4
r2b1	2	R	2022-03-28	6.87	41.6	3.1	6.33	3
r2b2	2	R	2022-03-28	6.96	41.2	3.2	6.32	4
nr2b1	2	NR	2022-03-28	7.21	41.7	3	6.45	2
nr2b2	2	NR	2022-03-28	7.55	41.8	3.2	6.35	9
nr2b3	2	NR	2022-03-28	7.22	41.6	3.6	6.37	3
kb2b1	2	EC	2022-03-28	7.19	41.2	3.4	6.34	0
kb2b2	2	EC	2022-03-28	7.15	41.4	3.2	6.34	0
kb2b3	2	EC	2022-03-28	7.13	41.4	3.1	6.34	1
r3b1	3	R	2022-03-28	7	41.3	3.3	6.26	3
r3b2	3	R	2022-03-28	7.59	41.5	3.1	6.38	1
r3b3	3	R	2022-03-28	7.45	41.8	3	6.39	3
nr3b1	3	NR	2022-03-28	7.43	41.4	3.3	6.34	3
nr3b2	3	NR	2022-03-28	7.3	41.3	3.2	6.35	1
nr3b3	3	NR	2022-03-28	7.24	41.5	3.1	6.37	0
kb3b1	3	EC	2022-03-28	6.85	41.7	3.1	6.34	3
kb3b2	3	EC	2022-03-28	7.29	41.8	3.2	6.3	2
kb3b3	3	EC	2022-03-28	7.23	41.7	3.3	6.37	1
s1	1	C	2022-03-28	8.17	42.5	2.8	6.35	13
s2	2	C	2022-03-28	7.02	41.7	2.7	6.29	17
s3	3	C	2022-03-28	7.2	41.4	2.9	6.33	5
r1b2	1	R	2022-03-30	7.02	43.9	2.1	6.43	3
r1b3	1	R	2022-03-30	7.14	44	2.3	6.39	3
nr1b1	1	NR	2022-03-30	7.19	43.8	2.3	6.35	2
nr1b2	1	NR	2022-03-30	7.1	43.9	2.4	6.36	2
nr1b3	1	NR	2022-03-30	7.47	44	2.4	6.35	1
kb1b1	1	EC	2022-03-30	7.12	44	2.2	6.36	2
kb1b2	1	EC	2022-03-30	7.59	43.9	2.2	6.34	4
kb1b3	1	EC	2022-03-30	7.38	43.9	2.7	6.34	2
r2b1	2	R	2022-03-30	7.48	43.1	2	6.35	2
r2b2	2	R	2022-03-30	7.33	43.2	2.1	6.34	0
nr2b1	2	NR	2022-03-30	7.55	43	2.1	6.42	2
nr2b2	2	NR	2022-03-30	7.32	42.9	2.1	6.37	3
nr2b3	2	NR	2022-03-30	7.36	42.5	2.3	6.37	1
kb2b1	2	EC	2022-03-30	6.8	42.3	2.9	6.34	2
kb2b2	2	EC	2022-03-30	7.67	42.4	2.8	6.39	1
kb2b3	2	EC	2022-03-30	7.18	42.5	2.5	6.35	1
r3b1	3	R	2022-03-30	6.67	42.6	2.2	6.31	2
r3b2	3	R	2022-03-30	6.99	42.5	2.4	6.32	3
r3b3	3	R	2022-03-30	7.12	42	3	6.33	0
nr3b1	3	NR	2022-03-30	6.36	42.4	2	6.28	2
nr3b2	3	NR	2022-03-30	6.44	42.6	2.3	6.31	2
nr3b3	3	NR	2022-03-30	6.56	42.4	2	6.32	2
kb3b1	3	EC	2022-03-30	6.92	42.9	2.3	6.33	3
kb3b2	3	EC	2022-03-30	6.69	42.8	2.2	6.33	2
kb3b3	3	EC	2022-03-30	7.02	42.8	2.1	6.35	2
s1	1	C	2022-03-30	6.88	43.6	2.2	6.36	3
s2	2	C	2022-03-30	7.5	42.9	1.9	6.35	3
s3	3	C	2022-03-30	6.87	42.5	1.7	6.36	1
r1b2	1	R	2022-04-06	6.97	44.6	2.6	6.48	11
r1b3	1	R	2022-04-06	6.77	44.9	2.6	6.44	2
nr1b1	1	NR	2022-04-06	6.55	44.4	3	6.44	12
nr1b2	1	NR	2022-04-06	6.43	44.4	3.1	6.43	8
nr1b3	1	NR	2022-04-06	6.42	44.4	3.1	6.42	12
kb1b1	1	EC	2022-04-06	6.98	44.7	3.1	6.43	14
kb1b2	1	EC	2022-04-06	6.89	44.6	3.1	6.43	8
kb1b3	1	EC	2022-04-06	6.94	44.5	3.1	6.46	10
r2b1	2	R	2022-04-06	6.7	44.1	2.8	6.39	15
r2b2	2	R	2022-04-06	6.87	44	2.7	6.4	15
nr2b1	2	NR	2022-04-06	7.2	44	3	6.42	16
nr2b2	2	NR	2022-04-06	6.81	44	2.9	6.42	10
nr2b3	2	NR	2022-04-06	6.69	43.8	3.1	6.43	4
kb2b1	2	EC	2022-04-06	6.75	44.1	3	6.41	5
kb2b2	2	EC	2022-04-06	6.66	43.9	3	6.43	12
kb2b3	2	EC	2022-04-06	6.7	44	2.9	6.42	7
r3b1	3	R	2022-04-06	8.03	43.9	2.8	6.42	12
r3b2	3	R	2022-04-06	8.1	43.9	2.8	6.44	14
r3b3	3	R	2022-04-06	7.51	44.1	3.2	6.39	5
nr3b1	3	NR	2022-04-06	7.33	43.8	3.1	6.42	5
nr3b2	3	NR	2022-04-06	7.58	43.8	3	6.43	8
nr3b3	3	NR	2022-04-06	7.35	44.9	3	6.43	12
kb3b1	3	EC	2022-04-06	7.4	44	2.9	6.43	5
kb3b2	3	EC	2022-04-06	7.54	44	2.8	6.43	8
kb3b3	3	EC	2022-04-06	7.25	44.1	3	6.42	8
s1	1	C	2022-04-06	6.76	44.4	2.5	6.45	10
s2	2	C	2022-04-06	6.86	44	2.6	6.43	8
s3	3	C	2022-04-06	6.77	43.8	2.8	6.45	6
r1b2	1	R	2022-04-14	7.06	42.8	3.9	6.26	34
r1b3	1	R	2022-04-14	7.66	43.1	3.7	6.25	30
nr1b1	1	NR	2022-04-14	6.96	42.5	3.9	6.24	28
nr1b2	1	NR	2022-04-14	7.01	42.7	4.3	6.28	20
nr1b3	1	NR	2022-04-14	6.97	43.5	3.9	6.31	16
kb1b1	1	EC	2022-04-14	6.39	42.3	4	6.28	15
kb1b2	1	EC	2022-04-14	6.9	42.5	4.1	6.31	21
kb1b3	1	EC	2022-04-14	6.76	42.3	4	6.3	14
r2b1	2	R	2022-04-14	6.46	42.4	4	6.3	23
r2b2	2	R	2022-04-14	6.67	42.6	3.9	6.31	24
nr2b1	2	NR	2022-04-14	6.99	42.5	3.9	6.36	11
nr2b2	2	NR	2022-04-14	6.76	42.6	4.2	6.34	12
nr2b3	2	NR	2022-04-14	6.94	42.3	4.4	6.33	16
kb2b1	2	EC	2022-04-14	6.65	42.2	4.2	6.31	14
kb2b2	2	EC	2022-04-14	6.66	42.7	4	6.32	16
kb2b3	2	EC	2022-04-14	6.64	43.1	4.1	6.33	13
r3b1	3	R	2022-04-14	6.35	42.2	4.3	6.34	27
r3b2	3	R	2022-04-14	6.89	42.6	4.2	6.35	20
r3b3	3	R	2022-04-14	7.02	41.8	5	6.34	19
nr3b1	3	NR	2022-04-14	6.85	42.6	4.8	6.33	5
nr3b2	3	NR	2022-04-14	6.48	42.4	4.8	6.34	14
nr3b3	3	NR	2022-04-14	6.38	42.6	4.9	6.32	9
kb3b1	3	EC	2022-04-14	6.93	42.3	4.3	6.31	12
kb3b2	3	EC	2022-04-14	6.73	42.5	4.2	6.32	14
kb3b3	3	EC	2022-04-14	6.87	42.3	4.2	6.32	12
s1	1	C	2022-04-14	7.38	42.4	3.4	6.3	21
s2	2	C	2022-04-14	6.93	42.5	3.6	6.33	9
s3	3	C	2022-04-14	6.9	42.4	4.2	6.32	16

Appendix C
Hatching rate, accumulation of clay and others full data set

ID	Site	Treatment	Sampling date	Water depth (cm)	Dominating substrate size (cm)	Subdominating substrate size (cm)	Clay particles (%)	Hatching rate (%)	Living alevins (count)
r1b2	1	R	2022-05-05	51	2 - 10	40 - 200	2.37	99	45
r1b3	1	R	2022-05-05	42	2 - 10	40 - 200	1.38	97	59
nr1b1	1	NR	2022-05-05	43	2 - 10	40 - 200	2.49	99	9
nr1b2	1	NR	2022-05-05	48	2 - 10	0.2 - 2	2.01	99	41
nr1b3	1	NR	2022-05-05	54	2 - 10		1.95	100	39
kb1b1	1	EC	2022-05-05	31	2 - 10	10 - 20	1.62	100	5
kb1b2	1	EC	2022-05-05	31	2 - 10		2.28	99	42
kb1b3	1	EC	2022-05-05	31	2 - 10		2.21	100	0
r2b1	2	R	2022-05-05	71	2 - 10	40 - 200	2.58	100	52
r2b2	2	R	2022-05-05	74	2 - 10	40 - 200	2.59	100	59
nr2b1	2	NR	2022-05-05	38	2 - 10	10 - 20	1.79	99	29
nr2b2	2	NR	2022-05-05	32	2 - 10	10 - 20	2.79	100	27
nr2b3	2	NR	2022-05-05	35	2 - 10	10 - 20	1.64	100	69
kb2b1	2	EC	2022-05-05	26	2 - 10		1.59	98	55
kb2b2	2	EC	2022-05-05	26	2 - 10		1.51	100	65
kb2b3	2	EC	2022-05-05	26	2 - 10		1.67	99	51
r3b1	3	R	2022-05-05	44	2 - 10	0.2 - 2	1.38	83	27
r3b2	3	R	2022-05-05	54	2 - 10	0.02 - 0.2	1.57	87	21
r3b3	3	R	2022-05-05	48	2 - 10	0.2 - 2	2.00	88	20
nr3b1	3	NR	2022-05-05	28	2 - 10	20 - 30	1.98	89	53
nr3b2	3	NR	2022-05-05	30	2 - 10	10 - 20	1.32	85	49
nr3b3	3	NR	2022-05-05	49	2 - 10	10 - 20	1.61	91	55
kb3b1	3	EC	2022-05-05	33	2 - 10		1.67	92	76
kb3b2	3	EC	2022-05-05	33	2 - 10		2.23	99	60
kb3b3	3	EC	2022-05-05	33	2 - 10		1.46	80	47