

## REVIEW

# Environmental threats and conservation implications for Atlantic salmon and brown trout during their critical freshwater phases of spawning, egg development and juvenile emergence

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**Abstract**

Atlantic salmon *Salmo salar* L. and brown trout *Salmo trutta fario* L. are species of high socio-economic and ecological value. Declining populations make them target species of fisheries management. This paper reviews the direct effects of deficient longitudinal connectivity, changes in discharge, high water temperatures, oxygen depletion, changes in water chemistry and increasing loads of fine sediment on the critical life stages of spawning, egg incubation and emergence. It further provides an overview about the basic autecological requirements of Atlantic salmon and brown trout and summarises important thresholds of physico-chemical tolerances. This collection of information provides important baselines for assessing historical, ongoing and new threats relevant for the management of both species in fresh waters. Critical early-life stages of both species are almost identical, creating synergies in conservation and restoration. Seaward-migrating forms are exposed to further stressors, but improving starting conditions can also greatly improve their resilience.

**KEYWORDS**

climate change, fisheries management, river restoration, *Salmo salar*, *Salmo trutta*, spawning ground

## 1 | INTRODUCTION

Atlantic salmon *Salmo salar* L. and brown trout *Salmo trutta fario* L. are species of high socio-economic value related to human consumption and recreational fisheries (Butler et al., 2009; Elliott, 1989; EUMOFA, 2019; Lobón-Cerviá, 2017; Pokki et al., 2018). They also play important ecological roles in the functioning of freshwater and marine ecosystems (Hastie & Cosgrove, 2001; Reimchen, 2018; Taeubert & Geist, 2017; Willson & Halupka, 1995) and are considered indicator species in watercourse quality assessments and restoration (Pander & Geist, 2010; Pander et al., 2009; Soulsby et al., 2001; Vehanen et al., 2010a). Thus, the conservation and

maintenance of sustainable populations of these species is of important economic and political interest.

Atlantic salmon and brown trout are representatives of the genus *Salmo* (Webb et al., 2007). Atlantic salmon is native to the North Atlantic area, and its indigenous distribution range in Europe extends from Iceland eastwards to the Baltic Sea and the Pechora river in the northwest of Russia, and southwards to the British Isles and the Douro river in northern Portugal (Figure 1; MacCrimmon & Grots, 1979). The species exhibits differing life strategies throughout its range in the North Atlantic. Depending on the degree of seaward migration, life strategies can be roughly classified as complete anadromous (Figure 2), incomplete anadromous and non-anadromous

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(also referred to as landlocked), but uncertainties and variations with regard to aspects of the life cycle remain (Webb et al., 2007). The “classical” *Salmo salar*, which is the focus of this review, is the anadromous form, living in the sea and migrating to its natal rivers to spawn. Juveniles spend up to five years in fresh water before migrating to sea to mature (Hutching & Jones, 1998). The time of spawning migration can vary between sexes and geographically with fish spending several winters at sea (multi-sea-winter fish) versus the so called grilse that only spend one winter at sea (Porter et al., 1986).

Brown trout is native to Europe with a distribution range that extends from Iceland eastwards to northern Scandinavia and Russia and southwards to the Atlas Mountains, the Ural Mountains and the Aral Sea basin (Figure 1; Jonsson & Jonsson, 2011; Williams & Aladin, 1991). *Salmo trutta* can be divided into several subspecies, morphotypes or ecophenotypes that can exhibit distinctive life histories, particularly when it comes to migration directions and habitat preferences of adults. Most commonly, the species is subdivided into *Salmo trutta trutta* (adults living in the sea and migrating to rivers for spawning), *Salmo trutta lacustris* (living in lakes and migrating to lake tributaries for spawning) and *Salmo trutta fario* (a resident form spending its whole life cycle in rivers with migrations to spawning grounds within the river system), which is the most common form and the focus of this review (Figures 2 and 3; Kottelat & Freyhof, 2007).

Atlantic salmon has experienced widespread population declines and extirpations over the last century (Parrish et al., 1998). Throughout its range (stocks in 2359 rivers), 43% of *Salmo salar* populations are at risk, threatened or heavily declining (NASCO, 2018, 2019). Only 14% of rivers have sustainable stocks, and notably, 36% of rivers have no available data to assess stock status, some of which (particularly in Southern Europe) may be near extinction (NASCO, 2019). While the global IUCN conservation status of Atlantic salmon (least concern; last assessed 1996) is in need of an update (World Conservation Monitoring Centre, 1996), more recent assessments in Europe have classified Atlantic salmon as vulnerable (Freyhof, 2014). Atlantic salmon is already considered extinct in Belgium, Netherlands, Germany, Czech Republic, Poland, Slovakia and Switzerland, and many populations have been lost from Ireland,

Wales, Scotland, England, Iberian Peninsula, France, Denmark, Sweden, Norway and European Russia. Most recovery plans for Atlantic salmon have been running for more than 20 years and are still characterised by frequent stocking (ICES, 2019c; ICES, 2017a; Monnerjahn, 2011).

Brown trout (*Salmo trutta fario*) is classified “least concern” on the IUCN Red List in Europe (Freyhof, 2011). Decreasing population trends for *Salmo trutta fario* are reported from its southern distribution range, for example Spain as vulnerable (Doadrio, 2001) and Andalusia as endangered (Ruíz & Rodríguez de los Santos, 2001), mostly due to climatic change. However, the intense and routine stocking of brown trout practised throughout Europe since the beginning of the 20th Century may potentially be masking the real status of natural populations (Bernaś & Waś-Barcz, 2020).

As a result of their variable life-history strategies, the threats affecting the population status of Atlantic salmon and brown trout can also be diverse (Dudgeon, 2019), making selection of the most appropriate management and conservation measures complex. The basis for healthy, resilient and sustainable populations of brown trout and Atlantic salmon is already set during their critical early-life stages (egg incubation, early development) in fresh water. The conditions for egg and larval development can strongly influence subsequent growth, survival and reproductive fitness (Russell et al., 2012). This is a critical bottleneck for both resident freshwater and sea-migrating populations, since only healthy smolts are sufficiently robust to withstand the manifold threats that they encounter on their way to the sea, in estuaries and intertidal areas (Lauridsen et al., 2017), and within the marine environment. In these habitats, it is known that fish can be easily infected with fish diseases (e.g. complex gill diseases) and parasites (e.g. sea lice *Gyrodactylus salaris*) originating from salmon farming (Rosenberg, 2008) or escaped farmed salmon (Rozas-Serri, 2019). For more information on marine threats on salmon, see Parrish et al. (1998) and Forseth et al. (2017). Identifying the threats affecting the critical life stages of brown trout and Atlantic salmon during their early freshwater life stages can be hence seen as prerequisite to sustain healthy populations. In fresh water, local factors such as interruption of migration

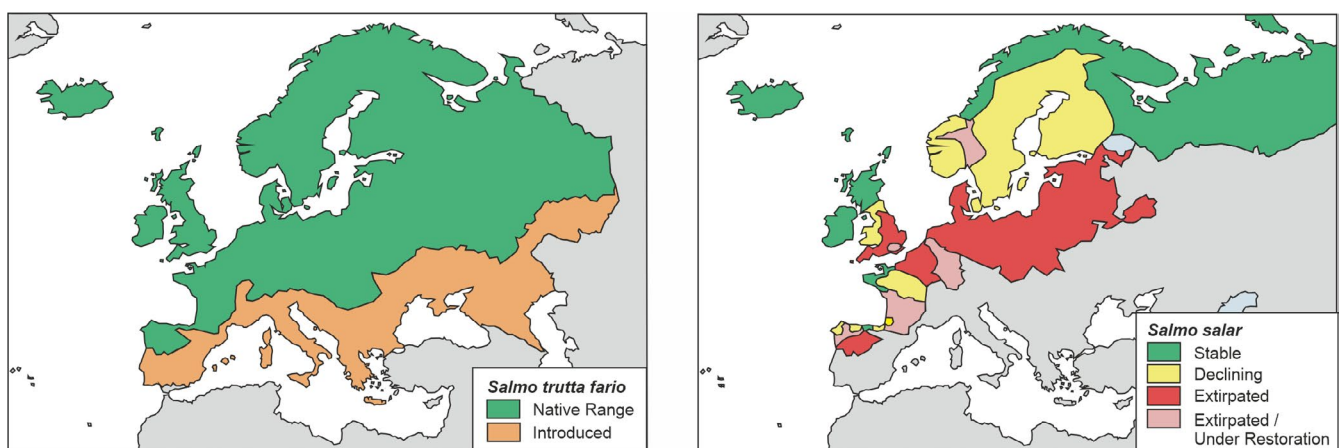
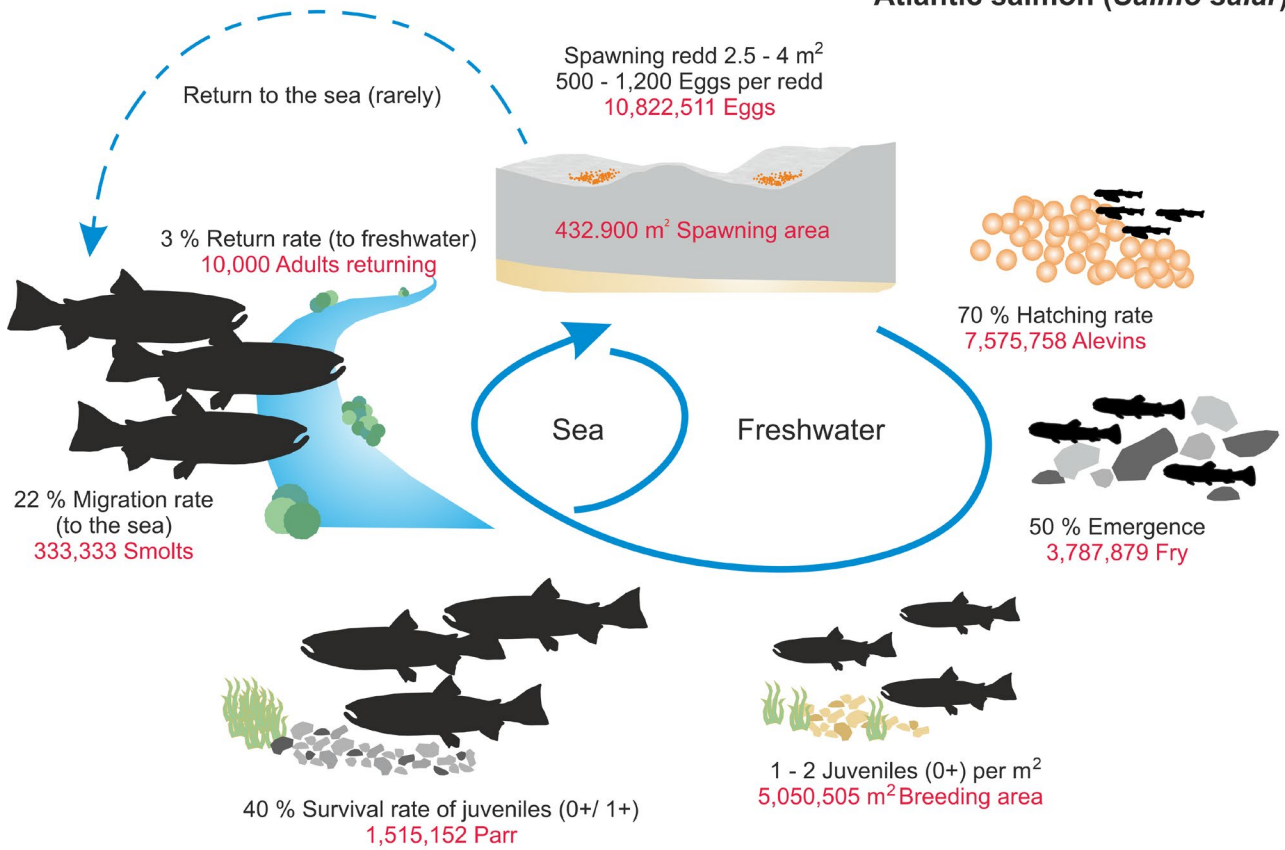


FIGURE 1 Distribution range of brown trout (*Salmo trutta fario*) and Atlantic salmon (*Salmo salar*) in Europe

**Atlantic salmon (*Salmo salar*)**



**Brown trout (*Salmo trutta fario*)**

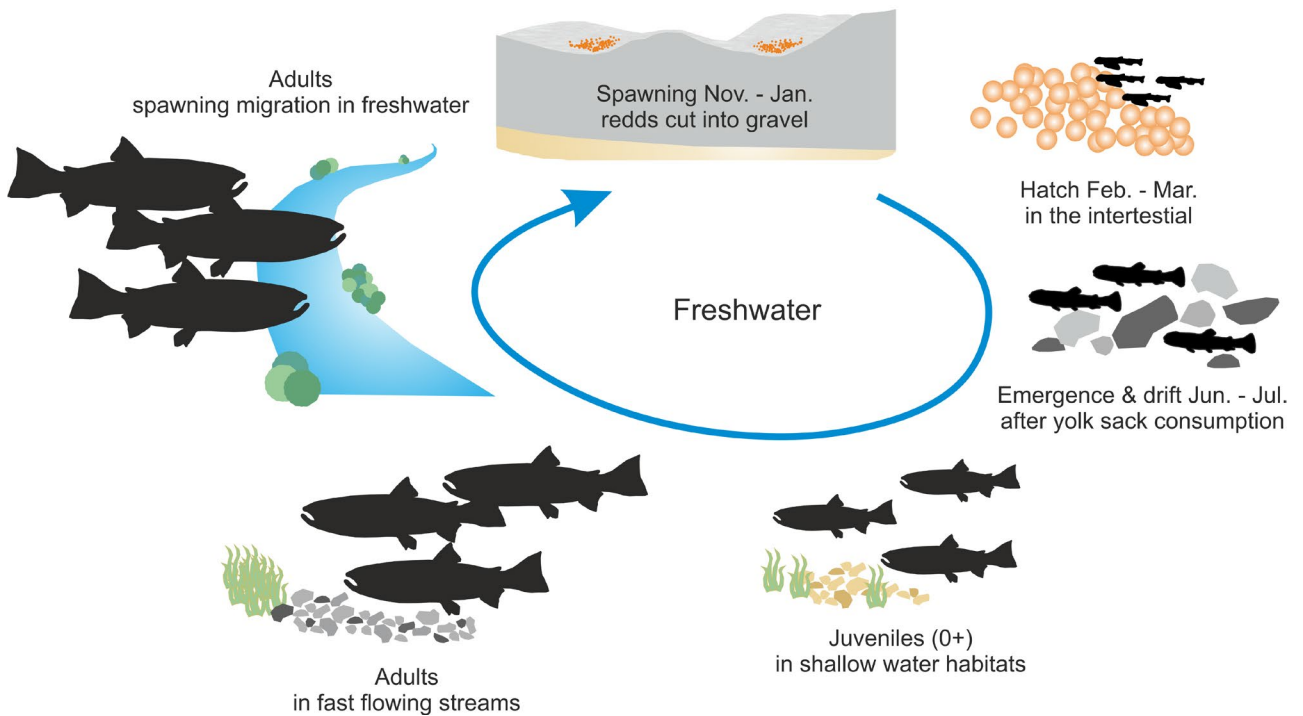
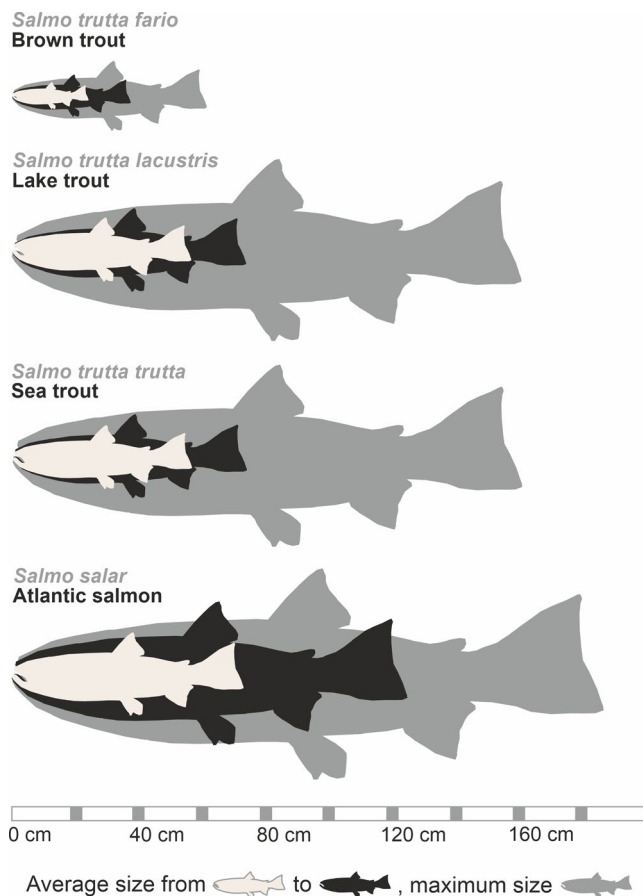


FIGURE 2 Common life cycles of Atlantic salmon and brown trout. Atlantic salmon life cycle includes the survival rates at different development stages and details on the required area during spawning and juvenile phase (numbers C. Wolter, pers. comm.)



**FIGURE 3** Size variation and overlap between and within different mature salmonid species which can co-occur in the same spawning habitat. Brown trout: 20<sup>1</sup>–30<sup>1</sup> cm, 50<sup>2</sup> cm; lake and sea trout: 45<sup>1</sup>–60<sup>1</sup> cm, 130<sup>2</sup> cm; Atlantic salmon: 60<sup>2</sup>–100<sup>2</sup> cm, 150<sup>2</sup> cm. All sizes provided as standard length (SL). Sources: <sup>1</sup>Kottelat and Freyhof (2007); <sup>2</sup>Gerstmeier and Romig (2003)

routes, habitat degradation and pollution are known to impair sustainability of stocks or even cause local extinctions (Forseth et al., 2017; Hoffmann, 1996; Jonsson & Jonsson, 2009; Lenders et al., 2016; Wolter, 2014). While most of these threats act systemically, their mitigation mostly needs to be addressed locally (e.g. in relation to barriers to migration, water quality or habitat availability). This includes restoration measures such as the creation of spawning grounds and juvenile habitats or facilitating connectivity (Geist & Hawkins, 2016).

To address these threats effectively, it is important to understand the mechanisms of how single factors and their interactions affect the respective life cycle stages and which mitigation measures are most effective (Geist, 2015). Due to their cultural and economic importance, the number of research programmes on the biology of Atlantic salmon and brown trout, and thus scientific papers, has advanced dramatically over the years, calling for a systematic update on current knowledge and an assessment of past, present and emerging challenges related to the conservation of both species.

This paper aims to provide a comprehensive overview of the latest knowledge on: (i) the general autecological requirements of the critical life stages of Atlantic salmon and brown trout, namely spawning, egg incubation and emergence; (ii) the effects of deficient longitudinal connectivity, changes in discharge, high water temperatures, oxygen depletion, changes in water chemistry and increasing loads of fine materials on those life stages; and (iii) important thresholds of their physico-chemical tolerances. Based on the results of this review, historical, ongoing and new threats in freshwater are discussed, and implications for future conservation and management actions of both species in freshwater are proposed.

## 2 | GENERAL HABITAT REQUIREMENTS

### 2.1 | Water body connectivity

Biological connectivity relates to four dimensions in riverine ecosystems: longitudinal, lateral, vertical and temporal (Ward, 1989). The linear connectivity or linear continuity of watercourses is particularly important for diadromous species like Atlantic salmon and sea trout (Aarestrup & Koed, 2003; Finstad et al., 2005). Migration between spawning areas/sites of hatching, juvenile habitats and the sea is crucial for the survival of these species and must be unhindered. The ability to overcome an obstacle depends mainly on the type and height of the barrier, the tailwater depth, the body length of the fish, its behaviour and its life stage (Birnie-Gauvin et al., 2019; Kemp, 2012; Kemp & O'Hanley, 2010). For upstream movements, especially the tailwater depth (pool below the barrier) plays a critical role in enabling passage. All this information is also key for designing suitable mitigation (Kemp, 2012; O'Hanley, 2011; Silva et al., 2018; Venus et al., 2020). Ideally for adult fish, the tailwater depth should be 1.25 times the height of the species to allow passage (Stuart, 1962). Atlantic salmon can jump up to 1.5 m and overcome higher obstacles than brown trout due to their larger size (Gerlier & Roche, 1998). Furthermore, they have a higher swimming capacity (Peake et al., 1997). In steep riffles, water depths of twice to three times the body height are regarded as a minimum for successful passage for both species. Shorter distances (<2 m) can also be passed in water depths at body height (DWA, 2014; LfU, 2005).

Lateral connectivity, in turn, ensures a network between rivers and laterally located aquatic habitats such as nutrient-rich floodplains or backwaters, generally increasing the overall productivity of the riverine ecosystem (Opperman et al., 2017; Pander et al., 2018). This also increases the food availability for different fish species such as salmonids.

Vertical connection exists between the interstitial spaces, the riverbed, the groundwater and the open water. The hyporheic zone is a key habitat for successful egg and larval development of salmonids (Malcolm et al., 2003a,b; Mueller et al., 2014; Sternecker et al., 2013a,b). Eggs and yolk sac larvae find suitable hydraulic conditions in the interstitial spaces, which offer them not only protection against predators and external influences, but also enables optimal

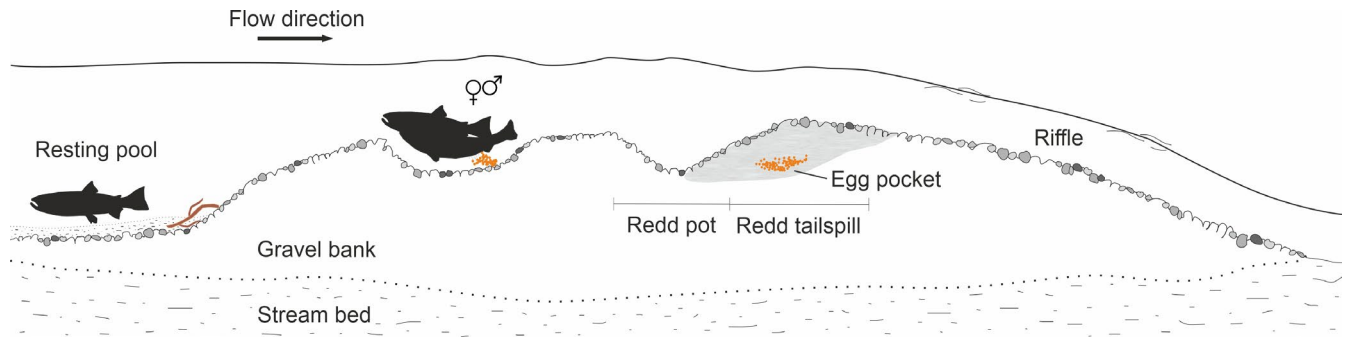


FIGURE 4 Important features of Atlantic salmon and brown trout spawning grounds

oxygen supply and the disposal of toxic metabolites such as ammonium (Brunke, 1999; Chapman, 1988; Crisp, 1993; Greig et al., 2007; Kondolf et al., 2008).

The temporal dimension represents the varying connectivity with time, for example high or low flow events during different seasons (Ward, 1989). Atlantic salmon and brown trout, as with many other species, have developed and diversified species-specific life-history strategies to adapt to these temporal changes, for example spawning in autumn or spring, migratory or resident species (Sternecker et al., 2014).

The required water body size between riverine ecosystems for a successful development of a fish population is difficult to measure. In general, the distance between essential habitats that need to be accessible during specific life stages, seasons or daytime as well as prey availability are seen as main factors in determining the home range and total distance covered by a species and can be highly variable. During the spawning period, most salmonid species migrate upstream into their natal rivers.

The anadromous form of Atlantic salmon is considered a long-distance migrator of up to 700 km (Cuinat & Bomassi, 1987). Migration distance generally depends on the life stage and season (e.g. rearing, feeding, overwintering, spawning migration). By contrast, non-anadromous freshwater-resident populations (mostly landlocked) or male parr can also mature in the absence of a seaward migration (Hutchings et al., 2019). Such forms occur throughout the distributional range of Atlantic salmon in North America (MacCrimmon & Gots, 1979; Power, 1958) and northern Europe (Berg, 1985; Davidsen et al., 2020; Kazakov, 1992; MacCrimmon & Gots, 1979). Some of these resident freshwater populations show deviant spawning behaviour such as spawning in lakes (Verspoor & Cole, 2005), or in lake inlets and outlets (Gibbins et al., 2002).

Brown trout can spawn in the main stems of a river system like Atlantic salmon, but generally prefer smaller streams (Crisp, 2000), often leading to spatial segregation of the two species (Geist et al., 2006). The water bodies used by brown trout for spawning are usually about 3–5 m wide and about 50 cm deep, with a gradient of up to 5% (Crisp, 2000; Jonsson & Jonsson, 2011). Brown trout has also been observed in small tributaries with a width of less than 1 m and an average annual discharge of 30–40 L/s during spawning

(Geist et al., 2006; Jonsson et al., 2001). Landergren (2004) even found spawning sites in waters that periodically dry out, but only when juveniles could migrate to the main stem. Resident brown trout do not need a connection to the sea to fulfil their life cycle, in contrast to its ecophenotype, the sea trout. Sea trout spend their growth phase in coastal marine waters until they return to spawn in their natal river (ICES, 2013; Klemetsen et al., 2003; Thorstad et al., 2016). Another ecophenotype, the lake trout, typically migrates from pre-Alpine lakes into tributaries for spawning (Denic & Geist, 2010; Klemetsen et al., 2003). Both types have similar requirements for water body size and freshwater passability as the anadromous Atlantic salmon (Aarestrup & Koed, 2003; Finstad et al., 2005; Klemetsen et al., 2003). They can undertake extensive spawning migrations, which can exceed 100 km, or occasionally even >500 km, the same as recorded for sea trout (Klemetsen et al., 2003; Thorstad et al., 2016). Resident brown trout usually undertake smaller spawning migrations within a river or stream system, but if suitable spawning sites are missing in the immediate vicinity, spawning migrations can also reach up to 100 km (Jungwirth et al., 2003; Olsson et al., 2006).

## 2.2 | Discharge and water depth

Discharge and its dynamics are crucial for the reproduction of brown trout and Atlantic salmon in rivers and streams. For Atlantic salmon and sea trout, flow events have been described to stimulate the entry into their natal rivers, often coupled with other environmental factors (Banks, 1969; Clarke et al., 1991; Erkinaro et al., 1999; Jonsson, 1991; Jonsson et al., 2018; Smith et al., 1994; Svendsen et al., 2004; Thorstad et al., 1998). A rare exception to this observation is the study from Davidsen et al. (2013) conducted in Norway, which could not confirm that river entry of Atlantic salmon was facilitated by increased water discharge and/or ebb tide.

Atlantic salmon prefer to spawn in the main stream of rivers and large tributaries with an average annual discharge of >1 m<sup>3</sup>/s and a gradient of >3% (Bergheim & Hesthagen, 1990; Mills, 1989). Literature on the average runoff rates at spawning grounds of Atlantic salmon and brown trout was reviewed by Louhi et al. (2008).

Discharge data from brown trout streams vary between  $<1.0$  and  $350 \text{ m}^3/\text{s}$ , and data on salmon streams between  $0.5$  and  $300 \text{ m}^3/\text{s}$  depending on whether the fish spawn in small tributaries or in the main stream.

Water depth is crucial during migration and spawning, where the fish alternate between active swimming at various depths, spawning in rather shallow riffle stretches and resting in sheltered pools. Resting in a given pool can last up to 2–3 months (Webb, 1989). Low discharge may decrease the quantity and quality of important habitat features. Spawning of Atlantic salmon and brown trout mainly occurs at water depths between  $0.5$  and  $1 \text{ m}$  (reviewed by Smialek et al., 2019), and resting pools should have a minimum depth of  $>0.9 \text{ m}$  (Moreau & Moring, 1993).

### 3 | SPAWNING AND REARING HABITAT REQUIREMENTS

The spawning and rearing habitat requirements of Atlantic salmon and brown trout overlap to a large extent (see reviews by Heggberget et al., 1988; Klemetsen et al., 2003; Smialek et al., 2019), so that spawning sites can overlap wherever both species occur together and suitable habitat exists.

Spawning of both species in central European latitudes takes place between November and January and local spawning events extend over two to three weeks (Armstrong et al., 2003; Crisp, 1993). According to Heggberget et al. (1988), spawning in streams with sympatric populations is partly separated by timing. There, spawning season of brown trout starts earlier, with peak spawning occurring two weeks before that of Atlantic salmon (Crisp, 1993; Heggberget et al., 1988). Nevertheless, spawning time can vary locally and may overlap as evident from regular appearance of hybrids (Hartley, 1996; Matthews et al., 2000; Westley et al., 2011; Youngson et al., 1992).

Salmonids in general require spawning habitats with a gravel bottom and a high exchange between the open water and the interstitial zone for successful reproduction (Kondolf, 2000; Malcolm et al., 2003a,b; Sternecker et al., 2013a,b). Thus, the spawning habitats of Atlantic salmon and brown trout are typically characterised by a pool riffle sequence (Figure 4).

At the transition to shallow overflowing gravel riffle stretches, the females cut spawning redds into the riverbed (Figure 4). Before placing their eggs, females first use their anal fin to examine whether the current conditions are suitable (Crisp, 1993). Laying eggs and insemination by males occur at the same time. Thereby, successive fertilisation by several males in both species is common (Serbezov et al., 2010; Thompson et al., 1998). Genetic studies found that alternative mating strategies play a major role in Atlantic salmon populations but not in brown trout (Garcia-Vazquez et al., 2001). In Atlantic salmon, small, sexually mature males (precocious freshwater parr) can fertilise up to 40% of eggs with increasing success rate at decreasing abundance of competitors (Thomaz et al., 1997). This alternative mating strategy in Atlantic salmon ensures that even if spawning occurs

simultaneously with brown trout in sympatry, the offspring will predominantly be Atlantic salmon (Garcia-Vazquez et al., 2001).

After insemination, eggs are covered with gravel (gravel spawners, e.g. Crisp & Carling, 1989; Klemetsen et al., 2003; Louhi et al., 2008; Ottaway et al., 1981). Salmonids are stage spawners, cutting several redds one after the other. On average, redds are  $1\text{--}5 \text{ m}^2$  in size (Barlaup et al., 2008; Pulg, 2009). Although a relationship exists between female length and redd size, with larger females preparing larger redds (Heggberget et al., 1988; Ottaway et al., 1981), attribution of individual redds to species directly in the field is difficult (Dirksmeyer, 2008). The main reason is that the size ranges of Atlantic salmon and brown trout can overlap, that is smaller Atlantic salmon overlap in size with large brown trout (Figure 3). In this case, they may share spawning sites and create same redd sizes. This is further complicated when the spawning ground is also used by the other ecomorphs of *Salmo trutta* as they can become even larger and overlap even more with Atlantic salmon in size (Figure 3). In addition, factors like flow velocity, sediment density and redd superimposition can also influence the size of the redds (Dirksmeyer, 2008). Therefore, only the direct identification of spawners, a genetic analysis of deposited eggs, or hatched larvae allow clear species assignment in case of sympatric occurrence (Gross et al., 1996).

Brown trout lay their eggs at depths of approx.  $8\text{--}25 \text{ cm}$ , whereas Atlantic salmon tend to lay their eggs deeper at  $15\text{--}30 \text{ cm}$  (Crisp, 2000). In contrast to the large quantities of small eggs released by gravel-spawning cyprinids (e.g. *Chondrostoma nasus* (L.); Duerregger et al., 2018; Nagel et al., 2020), salmonids release small quantities (on average  $1600\text{--}1800$  eggs/kg female) of large eggs (brown trout approx.  $\varnothing 5 \text{ mm}$ ; Atlantic salmon approx.  $\varnothing 6\text{--}9 \text{ mm}$ ) (Aulstad & Gjedrem, 1973; Bardonnnet & Baglinière, 2000; Randak et al., 2006; Thorpe et al., 1984).

On average, salmon eggs need more time to hatch than brown trout under the same conditions (Crisp, 1993). The development time of brown trout and Atlantic salmon from egg to hatching depends on the average ambient temperature. Brown trout eggs hatch after  $1.5\text{--}5$  months or  $410\text{--}456$  degree days, and Atlantic salmon eggs after  $383\text{--}545$  degree days (Kottelat & Freyhof, 2007; Smialek et al., 2019).

The larvae stay in the interstitial spaces until their yolk sac is nearly absorbed. This process is dependent on the ambient water temperature and the size of the individual (Einum & Fleming, 2000; Ojanguren & Braña, 2003). Afterwards, they emerge simultaneously at night from the gravel and drift into shallower water areas with moderate current velocities where they spend their juvenile phase and change to exogenous feeding (Bardonnnet et al., 1993; McCormick et al., 1998).

#### 3.1 | Water temperature

For cold-stenothermic species such as salmonids, the temperature not only determines the spawning time (Klemetsen et al., 2003; Sternecker et al., 2014), but also has a direct effect on the survival

**TABLE 1** Literature overview on the optimum, lower critical range (LCR), upper critical range (UCR) and lethal limit of temperature for three critical life stages of Atlantic salmon (AS) and brown trout (BT)

Stage	Species	Temperature (°C)				Reference
		Optimum	LCR	UCR	Lethal limit	
Spawners	AS	6–8*				Vernidub (1963) cited in EIFAC (1969)
Spawners	AS			>21		EIFAC (1969)
Spawners	AS	1–6*				Reviewed by Alabaster and Lloyd (1982)
Spawners	AS	6–10*				Piper et al. (1982)
Spawners	AS	10–17				Piper et al. (1982)
Spawners	AS		0–7	22–33	<0 or >27.8	Reviewed by Elliott (1994)
Spawners	AS				27–28	Garside (1973)
Spawners	AS	9–17				Mantelman (1958) cited by EIFAC (1969)
Spawners	AS	6–20		20–34		Elliott (1981)
Spawners	AS	0–8*				Elliott (1981)
Spawners	AS	13–15				Nikiforov (1953) cited in EIFAC (1969)
Spawners	AS	16–17	<7	22	25–28	Crisp (1993)
Spawners	BT	1–2*				Vernidub (1963) cited in EIFAC (1969)
Spawners	BT			>21		EIFAC (1969)
Spawners	BT	4–19	0–4	19–25	23–30	Elliott (1981)
Spawners	BT	1–10*				Elliott (1981)
Spawners	BT	2–6*				reviewed by Alabaster and Lloyd (1982)
Spawners	BT	9–13*				Piper et al. (1982)
Spawners	BT	9–16				Piper et al. (1982)
Spawners	BT	7–9*				Mansell (1966) cited in Raleigh et al. (1986)
Spawners	BT	7–13*		25		Hunter (1973)
Spawners	BT		0–4	19–30	<0 or >24.7	Reviewed by Elliott (1994)
Spawners	BT	13–14	<4	19	21–25	Crisp (1993)
Eggs	AS				<0 or >16	Elliott (1981)
Eggs <sub>inc</sub>	AS	4–11		<12		Poxton (1991)
Eggs	AS	4–12				Crisp (1993)
Eggs <sub>inc</sub>	AS			16		Ojanguren et al. (1999)
Eggs	BT				<0 or >13	Elliott (1981)
Eggs	BT	7			12–13	Jungwirth and Winkler (1984)
Eggs	BT	0–10				Crisp (1993)
Eggs <sub>inc</sub>	BT			12	15.5	Crisp (1993)
Eggs <sub>inc</sub>	BT	2–13	<0	>15		Raleigh et al. (1986)
Eggs <sub>inc</sub>	BT	8–10		14–16	16–18	Ojanguren and Braña (2003)
Larvae	AS	4–12				Crisp (1993)
Larvae	AS			22		Ojanguren et al. (1999)
Larvae	BT				>22	Hunter (1973)
Larvae	BT	0–10				Crisp (1993)
Fry	BT				>25.46	Spaas (1960) cited in Raleigh et al. (1984)
Fry	BT	6.7–12.8			<4.5	Markus (1962) cited in Raleigh et al. (1984)
Fry	BT	7–15				Brown (1973) cited in Raleigh et al. (1984)

Note: Optimum for spawners divides into “preferred” temperature, which is the value fish choose freely when moving within a thermal gradient, and temperature range at spawning, marked with a “\*”.

Abbreviation: Eggs<sub>inc</sub>, eggs incubating.

and development of eggs, juveniles and adults (Crisp, 1993; Crisp, 1996). The metabolic rate, growth or oxygen supply, as well as many other vital physiological processes, depend on the ambient temperature. Temperature and the ionic environment, among other factors, are particularly important for the duration and quality of egg maturation and thus, for the reproductive success of salmonids (Atse et al., 2002; Jobling, 1997). In addition, sexual maturity and fertility are also influenced by temperature (Jonsson & Jonsson, 2009). A general literature overview on thermal limits for salmon and brown trout during their critical life stages is given in Table 1. The optimum temperature range for Atlantic salmon spans from 7–20°C (Table 1), within which maximal growth occurs at 16–17°C (Jensen et al., 1989). The optimum range for brown trout is 4–19°C (Table 1).

The development of eggs and larvae in brown trout and Atlantic salmon occurs in winter. Low temperatures ensure a high solubility of oxygen in the water and thus, an optimal supply for the brood (Crisp, 1993). The early-life stages are more sensitive to temperature fluctuations and high temperatures than emergent larvae and adult fish as temperature tolerance increases with fish age (Elliott & Elliott, 2010; Hayes, 1949; Rombough, 1988). During winter, temperature in the redds is often several degrees higher than in the open water

(Witzel & MacCrimmon, 1983). However, this can be strongly dependent on interstitial water exchange or possible groundwater upwelling at the spawning site (Kondolf & Wolman, 1993; Malcolm et al., 2003a). For example, Clark (1998) found a vertical temperature gradient of  $-3.7^{\circ}\text{C}/\text{m}$  in the river bottom. For brown trout, temperatures between 0 and  $10^{\circ}\text{C}$  are considered ideal for egg and larval development at a survival rate of 95% (Crisp, 1993). According to Crisp (1993), the optimal temperature range for salmon is very similar, but slightly higher at 4– $12^{\circ}\text{C}$  (>95% survival rate) (Crisp, 1993; Jensen et al., 1989; Smialek et al., 2019; Table 1).

### 3.2 | Oxygen saturation

Salmonids are highly dependent on a sufficient oxygen supply for successful egg and larval development (Chapman, 1988; Eklöv et al., 1999). Minimum required oxygen demands of the early-life stages can vary widely, depending on which endpoint is considered. According to Rubin and Glimsäter (1996), a minimum of 10 mg/L should be available to achieve >50% egg-to-fry survival. However, most authors agree that the eggs of brown trout and salmon can

TABLE 2 Literature overview on the optimum, lower critical limit (LCL) and lethal limit of oxygen levels for three critical life stages of Atlantic salmon (AS), brown trout (BT) and reported for both species (both)

Stage	Species	Oxygen (mg/L)			Additional information	Reference
		Optimum	LCL	Lethal limit		
Spawners	AS		<6.5			Johansson et al. (2006)
Spawners	BT	≥9		<3	≥10°C	Raleigh et al. (1986)
Spawners	BT		<4.5		20°C	Hunter (1973)
Spawners	both	>9	7			EU (1978)
Eggs <sub>inc</sub>	AS		<5			Gibson (1993)
Eggs <sub>inc</sub>	BT	10	<10	<9	Egg-to-fry survival	Rubin and Glimsäter (1996)
Eggs <sub>inc</sub>	BT		<2.7		At 5 cm depth; 43% hatching success	Sternecker et al. (2013a)
Eggs <sub>inc</sub>	BT	>6.9				Ingendahl (2001)
Eggs <sub>inc</sub>	both		<5			Everest et al. (1987)
Eggs <sub>inc</sub>	both	>7				Crisp (1996)
Eggs <sub>inc</sub>	both	>7			<12.5°C	Crisp (2000)
Eggs <sub>inc</sub>	both		<5			Crisp (1993)
Eggs <sub>inc</sub>	AS			<6		Lacroix (1985a)
Embryos	AS			<3.7	5°C, 77 days, LC <sub>50</sub>	Hamor and Garside (1976)
Embryos	AS			<3.9	10°C, 43 days, LC <sub>50</sub>	Hamor and Garside (1976)
Fry	AS	> 8			80% to 100% saturation	Liao & Mayo (1972)
Embryos	BT	7–10			at hatching	Louhi et al. (2008)
Fry	BT	>7	<3		<15°C	Raleigh et al. (1984)
Fry	BT	>9	<5		>15°C	Raleigh et al. (1984)
Fry	both		<3		15°C	Bishai, 1962

Abbreviation: Eggs<sub>inc</sub>, eggs incubating.





tolerate oxygen concentrations as low as 5 mg/L, at least for a short time (Crisp, 1993; Niepagenkemper et al., 2003). Generally, 7.0 mg/L oxygen at an incubation temperature of 12.5°C and a flow velocity of >100 cm/h (Crisp, 1996; Ingendahl, 2001; Sternecker et al., 2013a) are recommended for a successful development. The oxygen demand during egg development depends on the development stage, size, carotene content and blood vessel density of the embryo (Hayes et al., 1951; Ingendahl, 1999; Rubin & Glimsäter, 1996). An overview of the different literature values on oxygen demands during different stages of development is presented in Table 2. In general, the oxygen demand is highest shortly before hatching is highest (Crisp, 1993).

### 3.3 | pH effects

Brown trout and Atlantic salmon occur in silicate and carbonate waters with pH values varying between 7 and 8.5. Maximum fish productivity is expected at pH values between 6.5 and 8.5, and the safe range of 6–9 proposed by ORSANCO (1955) has found worldwide acceptance in national recommended water quality criteria for aquatic life (EPA, 2019; EU, 2006). The pH furthermore determines the solubility of ammonia or aluminium, which in high concentrations can be toxic to aquatic organisms (Crisp, 1993; Finn, 2007; Gensemer & Playle, 1999; Wauer et al., 2004).

Ammonium ( $\text{NH}_4^+$ ) in aqueous solution is in equilibrium with free ammonia ( $\text{NH}_3$ ). Rising pH values and temperatures shift the equilibrium towards ammonia. For salmonids, a general guide value of <0.03 mg/L for ammonium and <0.004 mg/L for ammonia (EU, 1978; Directive 78/659/EEC) applies. Various other references place the recommended threshold values for ammonia between 0.015 and 0.001 mg/L (IWB & IDUS, 2012).

Aluminium can be dissolved and mobilised from terrestrial soils, river sediments or mining at pH values below 4.5 (Eriksson, 1981; Forseth et al., 2017). High concentrations of aluminium in fresh water often occur after heavy rainfall or during snow melting (Henriksen et al., 1984). A pH value < 6 and total aluminium concentrations of >0.1 mg/L are mentioned as critical for the vitality and reproduction of fish in weakly mineralised waters (Lenhart & Steinberg, 1984).

### 3.4 | Substrate composition

Brown trout and Atlantic salmon favour similar substrate compositions for spawning, egg and larval development (Louhi et al., 2008; Ottaway et al., 1981; Walker & Bayliss, 2007). The average grain size at the spawning grounds of brown trout and Atlantic salmon is about 10% of their body length (Kondolf & Wolman, 1993). The formula provided by Crisp (1993) can be used to determine the maximum average grain size in which a female can still spawn, where  $P$  is the median grain size in mm and  $L$  the fish length in cm:

$$P = L \times 0.5 + 4.6$$

Crisp (1993) generally referred to a high tolerance to different substrate compositions and reported 20–30 mm average grain size as particularly suitable for brown trout and Atlantic salmon. In contrast, Louhi et al. (2008) reported an average use of grain sizes of 16–64 mm taking most available literature values into account. The values are understood to apply equally to both species, but with a distinction between large (> 10 m<sup>3</sup>/s) and small rivers (<10 m<sup>3</sup>/s) where in the latter the salmon show a slight preference for larger substrates of 32–128 mm.

Another important characteristic determined by substrate composition is the storage density. To enable successful egg development, the interstitial pore spaces must be large enough to provide sufficient space for the eggs and later the hatched larvae to be supplied with fresh water. On the other hand, the spaces should be small enough to fix the eggs for undisturbed incubation. Optimum storage densities for successful egg and larval development are achieved with grain size fractions of 16–32 mm (Pulg et al., 2013; Sternecker & Geist, 2010) with less than 5% fines (particles <4 mm in diameter; Raleigh et al., 1986).

## 4 | THREATS TO ATLANTIC SALMON AND BROWN TROUT

### 4.1 | Lack of longitudinal connectivity

To date, many efforts have been made to restore river connectivity, for example in the context of the targets set by the EU Water Framework Directive (WFD; EU, 2000). However, Grill et al. (2019) demonstrated that out of 29,688 European rivers, 60% are still considered non free flowing (considering rivers >10 km). Further, considering only rivers connected to the sea ( $n=3726$ ), 15% are considered non free flowing. Grill et al. (2019) argued that the percentage of disconnected rivers may be even higher as small dams are often not reported in the global river impoundment datasets. This would be in line with Belletti et al. (2020) who described that more than one billion barriers fragment European rivers.

The interruption of longitudinal connectivity through transverse structures (e.g. weirs, power plants and culverts) or consumptive water use can cause (i) interruption or prevention of movement and migration of aquatic organisms and (ii) habitat change or degradation. The consequences are manifold (Benejam et al., 2016). The lack of access to adequate spawning grounds can have a negative impact on the reproductive success and the stability of populations (Gosset et al., 2006; Johnsen et al., 2011). Lack of genetic exchange due to spatial separation may lead to genetic impoverishment of populations and limited adaptability to environmental stress (Bijlsma & Loeschcke, 2012; Klütsch et al., 2019). A high risk of being injured or dying is present during downstream passage as fish enter turbines, bypass devices, trash racks, spill or trash gates or after passage of overflowed weirs (e.g. Rytwinski et al., 2017 for review; Mueller et al., 2017; Bierschenk et al., 2018; Knott et al., 2019; Pflugrath et al., 2019; Geist, 2021).

In addition, there can be cumulative effects in waters with a number of transverse structures that need to be passed (Gowans et al., 2003; Peter, 1998). Further, obstacles, interrupted flow patterns in rivers or turbine passage may disorient migrating fish, and thereby delay migration and increase the risk of predation (Baisez et al., 2011; Jepsen et al., 1998; Poe et al., 1991). A delay in migration is often associated with exhaustion due to prolonged search times for suitable migration routes, which could negatively affect reproductive success (Caudill et al., 2007; Hinch & Bratty, 2000; McLaughlin et al., 2013). Furthermore, temporal mismatch situations can occur in the time of larval development, where suitable habitat conditions do not match the time of larval occurrence (Cushing, 1975; Cushing, 1990). Hence, interrupted migration routes can lead to a severe thinning of the migrating populations in the long term (Aarestrup & Koed, 2003; Lundqvist et al., 2008), with the risk of depressing them below the minimum viable size (Courchamp et al., 2008). However, it has to be noted that not all migration barriers are of anthropogenic origin. The reintroduction of, for example, Canadian and European beavers, which are known to build wooden dams into small- to medium-sized rivers, cause local conflicts with management actions to restore fish migration and habitat, particularly spawning grounds (Gaywood, 2018). Negative effects of river fragmentation on movements of fish were already recognised in the mid-18th century when the first fish pass in northern Europe was built (Birnie-Gauvin et al., 2019; Johnsen et al., 2011). Today, it is well-known that mitigation measures need to be adjusted to site-specific conditions and species-specific requirements to be functional. Practically, most equations on how to build suitable fish passes exist for salmonids (Birnie-Gauvin et al., 2019; Noonan et al., 2012). Fish passage efficiency reviewed from articles from 1960 to 2011 by Noonan et al. (2012) revealed that on average salmonid passage success was 61.7% for upstream and 74.6% for downstream movement. Best predictors for passage efficiency included type of fish pass and its length. Birnie-Gauvin et al. (2019) argued that low efficiencies resulted from trying to “fit fish into equations” whereby essential factors such as natural variations on species and ecosystem level are not considered. Further, effective monitoring is seldom standard procedure, and thus, restrictions in connectivity are often overlooked.

van Puijenbroek et al. (2019) found that viable populations of Atlantic salmon occurred mainly in rivers that were at least 85% accessible. In rivers where the population was extinct or restocking of juvenile salmon was practised, accessibility averaged only 25%. Restocking of Atlantic salmon in European rivers often occurs in high numbers and repeatedly over several years (HELCOM, 2011; ICPR, 2015; Wolter, 2014). However, van Puijenbroek et al. (2019) pointed out that reintroduction of the species has happened in inaccessible rivers and thus was insufficient as a measure on its own to re-establish a viable population. Indeed, facilitating longitudinal connectivity will not have any long-term effects, unless all essential requirements for the different life stages are taken into account, for example appropriate habitats for spawning, rearing and foraging

(Bond & Lake, 2003; Dynesius & Nilsson, 1994; Pander & Geist, 2013; Poff et al., 1997; Ward & Wiens, 2001).

Habitat degradation can lead to increased competition for the limited resources, for example high-quality spawning sites (Essington et al., 1998; Gortázar et al., 2012). Possible consequences of a competition for spawning ground are overlapping redds, washed out or destroyed eggs by overcutting of redds by other conspecifics or competitors from the sister species, which can result in high reproductive losses (Bardonnet & Baglinière, 2000; Rubin & Glimsäter, 1996).

At which point spawning site capacity is reached depends on different factors such as number of females ready to spawn and the quality of the location. However, it is possible to outline the approximate space or habitat capacity required using the following formula:

$$A_{sp} = \frac{N_t}{N_n} \times A_{nest} \times \alpha$$

$A_{sp}$  is the required spawning site space,  $N_t$  is the number of eggs to reach the desired target of returning spawners,  $N_n$  is the number of eggs per nest,  $A_{nest}$  is the area of one nest and  $\alpha$  is a factor considering the distance between nests, and nests and shore.

If, for example, 10,000 returnees from an Atlantic salmon population are considered as the desired target, the number of eggs originally laid at the spawning site would be approximately 10,822,511 ( $N_t$ ) (see Figure 2). Taking a conservative approach by assuming a redd size of 4 m<sup>2</sup> ( $A_{nest}$ ) and 500 eggs ( $N_n$ ) per redd and a space factor = 5, the resulting redd area would be 432,900 m<sup>2</sup> containing 10,822,511 eggs (C. Wolter, pers. comm.).

## 4.2 | Discharge change

The increase in managed flows and water levels in freshwater systems (e.g. to optimise hydropower production) can impair the highly adapted strategies of fish species to natural occurring flow regimes. A threat from changes in runoff dynamics usually prevails wherever most of the natural runoff is used for hydropower, industry, irrigation or fish hatcheries (Bunn & Arthington, 2002; Forseth et al., 2017; Haag et al., 2010; Nilsson et al., 2005). The runoff in a diversion channel of hydropower plants can be greatly reduced, especially during dry periods, as a higher proportion of water is guided to the turbine. Limited water in the diversion channel can negatively affect certain key habitats such as overwintering habitats and spawning grounds and, in addition, reduce the ability to migrate through the channel (Crisp, 1993; LfU, 2005; Webb et al., 2001). Both, rapid increasing or decreasing water discharge, for example in response to the power demand (hydropeaking), can have detrimental consequences for fish populations and communities, especially if the river shows a low level of heterogeneity where transition into alternative habitats is not possible (Boavida et al., 2015; Harby & Noack, 2013; Lobón-Cervía & Rincón, 2004; Schmutz et al., 2015). For less mobile



life stages, such as eggs and larvae, a rapid decrease in water poses the risk of stranding (Casas-Mulet et al., 2015; Saltveit et al., 2001).

Successful spawning migration and spawning can be impaired if water levels are lower than the fish body height and if flow or hydraulic conditions over barriers (natural or artificial) are not optimal. Flow events, which are considered to trigger migration behaviour of Atlantic salmon (Clarke et al., 1991), may not take place during low discharge. Without this initiation, river entry will be delayed or even prevented (Solomon & Sambrook, 2004; Tetzlaff et al., 2008). The migration itself may lead to a faster exhaustion or higher risk of predation (Quinn & Buck, 2001) as shallow areas need to be overcome and access to resting pools may be strongly limited. At the spawning site, the fish are very unlikely to spawn if the water depth and flow velocity are insufficient (Louhi et al., 2008; Webb et al., 2001). In addition, the washing out of fine material during redd cutting and the successful insemination of the eggs and their deposition into the interstitial zone can be impaired if the water levels and flow velocities are too low. There is furthermore a higher risk of desiccation of the spawning sites during the period of egg incubation, which can result in recruitment failure (Casas-Mulet et al., 2015; Saltveit & Brabrand, 2013). Other risks posed on eggs and larvae include the insufficient vertical exchange between the hyporheic zone and open water, which may lead to lower oxygen contents and accumulation of toxic metabolites. Parry et al. (2018) investigated the impact of flow on the overall distribution and density of redds along a river and found that under low flow conditions redds tended to be more aggregated in the middle river reaches. On the one hand, this may minimise the risk of desiccation or insufficient oxygen supply, but on the other hand, it can result in a highly competitive environment for the emerging fry (Jonsson et al., 1998). Wedekind and Mueller (2005) found that brown trout hatched earlier when there was an increased risk of desiccation. This behaviour could be beneficial as the larvae can move away from the risk of drying out, freezing, predation or being damaged by UV radiation (Battini et al., 2000; Crisp, 1993; Kouwenberg et al., 1999). Flow dynamics can also affect the timing and success of emergence, with potential consequences for population dynamics of 0+ juveniles (Bergerot & Cattaneo, 2017), if, for example, emerged fry do not reach suitable rearing habitats or are predated on.

Conversely, strong runoff peaks (flooding or reservoir flushing) may expose spawning sites to increased erosion (Barlaup et al., 2008; Crisp, 1989). Discharge peaks can lead to the seasonal unavailability of these habitats, particularly in isolated spawning grounds. If, in addition, these areas have only very limited fish passability such as spawning sites in the headwaters of dams, which can naturally be affected by reservoir flushing and short-term strong runoff fluctuations, entire generations may be absent from the population structure. This may ultimately contribute to the instability of the overall population. Such runoff fluctuations also pose a high risk to incubated eggs such as redd stranding. Barlaup et al. (1994) reviewed a 100-year data series on stranded Atlantic salmon and brown trout redds and found a relationship between the high proportions of stranded redds (23%) and the random occurrence of low water discharge rates at high frequencies (27% of the year). Further,

strong runoff peaks can lead to a destabilisation and mobilisation of substrate and thus flush eggs or larvae out of the interstitial zone or mechanically damage them by moving material between them (Crisp, 1989; Crisp, 1993; Elliott, 1976; Mills, 1971). Immediately after deposition, the eggs of brown trout and Atlantic salmon are very sensitive to physical shock (Crisp, 1990): drifting over a distance of 10 m can lead to a mortality rate of 50% (Crisp, 1990). Sensitivity gradually decreases after the eyed stage. When eggs and larvae are washed out, they can either become easy prey for predators or may reach unsuitable sites for further development (Crisp, 1990).

### 4.3 | High water temperatures

In small- and medium-sized watercourses, increased or critical water temperatures may occur due to discharges of domestic and industrial waste waters (Cairns, 1970; Kinouchi et al., 2007). Another factor that can lead to higher water temperatures is global warming. Rising water temperatures can affect fish at all levels of biological organisation through either direct or indirect changes in physiological and ecological processes (Graham & Harrod, 2009). In view of ongoing climate changes, Jonsson and Jonsson (2009) expected that the thermal niche of cold adapted species, such as brown trout and Atlantic salmon, will result in a shift in distribution further to the north and that species in the southern part of their distributional areas are likely to go extinct (Ellender et al., 2016). In Europe, this means the disappearance of these species from Portugal and Spain and their spread north and east along the north coast of the Russian continent (Jonsson & Jonsson, 2009). However, a growth model scenario for brown trout under possible future climate conditions by Elliott and Elliott (2010) revealed negative effects on trout growth would not be experienced until a water temperature increase of 4°C in winter/spring and 3°C in summer/autumn is reached. This study further suggested that small increases of temperatures in winter and spring can lead to an increase in mean-mass of pre-smolts and be beneficial for smolt growth. Larger smolts are considered more resilient and, according to Gregory et al. (2019), have a higher chance of return to their natal rivers after maturation at sea. By contrast, faster growth can also result in seaward-migrating younger and thus smaller smolts, as has been observed over recent decades, which is expected to result in higher marine mortality (Russell et al., 2012).

Since both species are winter spawners, an increase in water temperature can lead to a delayed spawning migration. Further, more extreme weather events are expected, which will cause large fluctuations in runoff rates, making river accessibility and spawning migration more difficult (Harrod et al., 2009; Jonsson & Jonsson, 2009). In addition, sexual maturity and fertility of Atlantic salmon and brown trout decrease with rising temperatures (Jonsson & Jonsson, 2009). Significant reduced fertility (<70% and 45%, respectively) and survival (40% and 13%, respectively) of ova were observed from fish exposed to 22°C for 4 and 12 weeks (King et al., 2003, 2007; Pankhurst et al., 2011).

Crisp (1993) reported that during egg incubation at temperatures above 12°C, 50% of the eggs die and that no eggs survive

at temperatures above 15.5°C. Similar findings were reported by Ojanguren et al. (1999) where 16°C was established as the thermal limit for pre-hatching stages and 22°C for hatched larvae. Moreover, high water temperatures can lead to premature consumption of the yolk sac (Ojanguren et al., 1999). Further, the transition of the larvae from endogenous to exogenous food intake may not coincide with the time of occurrence of the prey (mismatch), and the larvae would not find suitable food after emergence and could starve (Arevalo et al., 2018; Cushing, 1990).

In addition, temperature, together with salinity, determines the physical properties of water, the amount of dissolved oxygen, the crystalline structure of various substances and the solubility properties of water. This in turn can influence the biochemical and toxicological effects of dissolved gases, solids, antibiotics and xenobiotics with probably negative consequences for the development of salmonids (Arias et al., 2002; Cousins & Jensen, 1994; Honkanen et al., 2001; Oppen-Berntsen et al., 1990).

#### 4.4 | Lack of oxygen

Oxygen deficiency can be caused by various factors, including oxygen-depleting microbial processes and algae blooms as a result of eutrophication and excessive temperatures, low discharge and clogged pores in the hyporheic zone. As the solubility of oxygen is directly related to the ambient water temperature, the concentration decreases when the temperature rises. At an air saturation in water of 80% and a water temperature of 5°C, approx. 10 mg/L of oxygen is dissolved in water. At 20°C, there is only 7 mg/L oxygen (Crisp, 1993). Hypoxic conditions (<7 mg/L dissolved oxygen) can cause die-off events of spawning salmonid species if high fish densities and low stream flows occur simultaneously, even in rivers with cold thermal regimes (Sergeant et al., 2017; Tillotson & Quinn, 2017).

The oxygen concentration in the hyporheic interstitial depends strongly on temperature, flow velocity, permeability of the sediment and consumption by organic processes. Embryo mortality can also occur by dominant ascending hypoxic groundwater (Malcolm et al., 2008). Long-term hypoxia (<3.7 mg/L oxygen) can lead to egg death or significant delays in development and thus to malformations and metabolic disorders (Hamor & Garside, 1976). Larvae are less prone to oxygen deficiency than eggs, as they are mobile and able to relocate to oxygen-rich areas (Crisp, 1993) or adjust their breathing frequency (Quinn, 2005). However, premature hatching of larvae may occur (Czerkies et al., 2001).

#### 4.5 | Extreme values in pH, aluminium and ammonium

Aquatic ecosystems can become acidified through natural processes in the bio- and geosphere (e.g. volcanism or natural pyrite oxidation) as well as through anthropogenic sources (atmospheric deposition

of acidity "acid rain" or pyrite oxidation from mining, agriculture and forestry) (Cresser & Edwards, 1987; Geller & Schultze, 2009). Spring floods, heavy rainfall events or snow melting can further promote acid discharges into water bodies (Serrano et al., 2008). Areas that are prone to water acidification due to their low buffer capacity include siliceous, low calcareous aquatic systems, which are often populated by Atlantic salmon and brown trout.

Extreme pH values below 6 or above 9 are particularly harmful as they can mobilise or activate other toxic substances (Crisp, 1993; Finn, 2007; Gensemer & Playle, 1999; Wauer et al., 2004). Both, ammonia in combination with high pH values, and dissolved aluminium in combination with low pH values, are particularly toxic to salmonids and other fish (Gensemer & Playle, 1999; Havas & Rosseland, 1995; Henriksen et al., 1984; Parkhurst et al., 1990; Wood & McDonald, 1987). The optimum pH range for adult brown trout and Atlantic salmon is between pH 6 and 9 (Table 3). Lethal limits are reached below pH 5 for all life stages. However, eggs, alevins and fry of Atlantic salmon and brown trout are considered more susceptible to the negative effects of low pH than adult fish (Jensen & Snekvik, 1972). The uptake of high H<sup>+</sup> levels disturb the ion-regulation in transcellular processes with its key toxic mechanisms occurring on the gills. It hinders the active uptake of sodium and stimulates efflux leading to an excessive production of mucus. (Leivestad & Muniz, 1976) and net losses of important electrolytes such as Na<sup>+</sup> and Cl<sup>-</sup> through the gills (Booth et al., 1988; Weatherley et al., 1989). The intracellular accumulation of aluminium affects transcellular processes, alters the carrier properties of the gill epithelium and reduces gill diffusion capacity causing respiratory distress (Exley et al., 1991; Havas & Rosseland, 1995). Increased aluminium uptake can thus lead to an imbalance in the body's metabolism (water-mineral and acid-base balance) and/or to suffocation (Wauer et al., 2004).

Both field and laboratory studies showed that a change in pH, especially in the early-life stages of salmonids, lead to high mortality rates (Grande et al., 1978; Schofield, 1976; Sternecker et al., 2013a,b). At pH values above 9, the egg stages of salmonids die before hatching (Crisp, 1993). The lower limit is 4.5 for Atlantic salmon, brown trout and lake trout (Crisp, 1993; Jensen & Snekvik, 1972). Peterson et al. (1980) found that salmon eggs in the ocular stage, which were kept at pH values between 4.0 and 5.5, hatched later or not at all because the low pH value probably inhibited the important hatching enzyme chorionase. Similar results were obtained earlier by Lacroix (1985a) and Lacroix et al. (1985b), who found the LL<sub>50</sub> to be reached at pH of 4.7 (lethal loading causing 50% mortality = LL<sub>50</sub>) in the interstitial water. Daye and Garside (1979) report that LL<sub>50</sub> for embryos is reached at pH 3.9, and for alevins at pH 4.3. They further claimed that long-term exposure of Atlantic salmon to pH < 4.5 will lead to a substantial decrease of populations or even extirpation in freshwater habitats.

Exposure to low pH leads to sublethal effects in vital organs such as the skin, liver, spleen and damage to blood vessels, gills, brain and retina (Daye & Garside, 1980). In general, at chronically low pH values of 4.7–5.4 in the water, annual juvenile fish productivity of Atlantic salmon is significantly lower than in waters with pH values

**TABLE 3** The optimum, critical and lethal concentrations of pH, aluminium, ammonium and ammonia for critical life stages of Atlantic salmon (AS), brown trout (BT) and reported for both species (both)

Stage	Species	Optimum	Additional information	References
Critical limits				
Spawners	BT	4.5–9.2		Crisp (1993)
Spawners	BT	6.8–7.8		Heacox (1974) cited in Raleigh et al. (1986)
Spawners	both	6–9		EU (1978)
Spawners	both	$\text{NH}_4^+ < 0.03 \text{ mg/L}$ and $\text{NH}_3 < 0.005 \text{ mg/L}$		EU (1978)
Eggs <sub>eye</sub>	BT	pH < 4.0, no $\text{Al}_i$ correlation observed	Mortality > 40%; field	Serrano et al. (2008)
Eggs <sub>inc</sub>	BT	$\text{NH}_4^+ < 1.5 \text{ mg/L}$	Mortality > 40%; field	Sternecker et al. (2013a)
Fry	BT	pH < 4.0, no $\text{Al}_i$ correlation observed	Mortality > 40%; field	Serrano et al. (2008)
Juvenile	BT	6.7–7.8	pH < 5.0 or > 9.5	Raleigh et al. (1984)
Lethal limits				
Spawners	AS	$\text{NH}_4^+ 0.2\text{--}0.5 \text{ mg/L}$	$\text{LC}_{50}$ after 24 h	Alabaster et al. (1979)
Spawners	BT	$\text{NH}_4^+ 0.6\text{--}0.7 \text{ mg/L}$	$\text{LC}_{50}$ after 96 h	Environment Canada and Health Canada (2001)
Spawners	BT	pH < 5 and $\text{Al}_{\text{tot}} > 100 \mu\text{g/L}$	Field	Barlaup and Åtland (1996)
Eggs <sub>eye</sub>	AS	pH = 4.0–4.5	Mortality 50%; >30 days	Peterson et al. (1980)
Eggs <sub>inc</sub>	AS	pH = 4.7	$\text{LL}_{50}$ ; field	Lacroix (1985a)
Eggs <sub>inc</sub>	AS	pH = 3.9	$\text{LL}_{50}$ ; lab	Daye and Garside (1979)
Eggs	AS	pH < 4.8–5.6 and $\text{Al}_i > 20\text{--}310 \mu\text{g/L}$	Egg-to-alevin mortality > 93%; lab	Skogheim and Rosseland (1984)
Eggs <sub>inc</sub>	AS	pH = 3.5	Mortality 100%; lab	Carrick (1979)
Eggs <sub>inc</sub>	BT	pH = 3.5	Mortality 100%; lab	Carrick (1979)
Eggs	BT	pH < 4.8–5.6 and $\text{Al}_i > 20\text{--}310 \mu\text{g/L}$	Egg-to-alevin mortality > 86%; lab	Skogheim and Rosseland (1984)
Eggs <sub>eye</sub>	BT	pH < 4.5	Mortality > 90%; lab	Brown and Lynam (1981)
Eggs <sub>inc</sub>	both	pH < 4.5 and pH > 9	Die before hatching	Crisp (1993)
Alevins	AS	pH = 4.3	$\text{LL}_{50}$ ; lab	Daye and Garside (1979)
Alevins	BT	$< 20 \text{ Al}_{\text{tot}} \mu\text{g/L}$	$\text{LC}_{50}$ ; field	Weatherley et al. (1990)
Fry	AS	pH < 5	Sublethal effects; lab	Daye and Garside (1979)
Fry	AS	pH < 5	Mortality > 70%; field	Lacroix (1985a)
Fry	BT	$\text{Al}_{\text{tot}} = 15 \mu\text{g/L}$	$\text{LC}_{50}$ ; 42 days; field	Weatherley et al. (1990)
Fry	BT	pH = 4.5 and $\text{Al}_i = 323 \mu\text{g/L}$	Mortality > 50%; >108 days; lab	Reader et al. (1991)
Fry	BT	pH = 4.5 and $\text{Al}_i = 324 \mu\text{g/L}$	Mortality > 50%; lab	Çalta (2002)
Fry	BT	pH = 4.5 and $\text{Al}_i = 600 \text{ nmol/L}$ and $\text{Ca} = 20 \mu\text{mol/L}$	Mortality > 90%; lab	Sayer et al. (1991)

Abbreviations:  $\text{Al}_i$ , inorganic monomeric aluminium;  $\text{Al}_{\text{tot}}$ , total aluminium; eggs<sub>eye</sub>, eggs eyed stage; eggs<sub>inc</sub>, eggs incubating;  $\text{LC}_{50}$ , lethal concentration with 50% mortality;  $\text{LL}_{50}$ , lethal loading causing 50% mortality.

above 5.6–6.3 (Daye & Garside, 1979). The critical threshold for first-year juvenile brown trout is 4.8–5.4 in streams rich in dissolved organic carbon (Serrano et al., 2008).

Recently hatched salmonids are regarded as particularly sensitive to ammonium (Table 3). A growth depression occurs at sublethal concentrations of 0.35–10  $\mu\text{M}$ , while long-term exposure to 1.4–5.3  $\mu\text{M}$  can lead to a reduction in the number of erythrocytes

and leukocytes as well as haematocrit and haemoglobin concentrations (Vosylinė & Kazlauskienė, 2004). A mortality rate of 50% ( $\text{LC}_{50}$ ) was observed in adult brown trout at a concentration of 0.6–0.7 mg/L after 96 h (Environment Canada & Health Canada, 2001) and in Atlantic salmon at 0.2–0.5 mg/L after 24 h (Alabaster et al., 1979). Effects on growth were observed in Atlantic salmon at a concentration of 0.037–0.065 mg/L  $\text{NH}_3$  (28 days, NOEC)

(Fivelstad et al., 1993). The critical limits and lethal limits reported in the literature for pH, ammonium and aluminium for both species and their critical life stages are summarised in the overview Table 3.

Even though acidification continues to be a problem, for example in parts of Scandinavia, recognition of the problem, measures of source control (e.g. flue gas desulphurisation) and targeted mitigation measures (e.g. liming), has resulted in a slow recovery today (Geller & Schultze, 2009).

#### 4.6 | Increased inputs of fine materials

The type, size and composition of the substrate determine whether the female can cut a suitable spawning redd, how deep and large it becomes, and how stable it remains for the period of egg ripening and larval development.

Anthropogenic influences, such as catchment land use with erosion-prone crops, forestry practices or overgrazing, can cause significantly increased levels of fine material inputs and the associated sedimentation rates of substances. In general, the introduction of anthropogenic fine material into freshwater systems are mainly caused by agriculture, logging and discharges from urban areas (Greig et al., 2005a; Hendry et al., 2003; Mueller et al., 2020; Zimmermann & Lapointe, 2005). Also, climate change and the change in cultivation to “energy crops” such as maize particularly promote soil erosion in agriculture and can cause fine sediment input into water bodies (Bierschenk et al., 2019). Net inputs from agriculture can be as high as 35–46.5 kg/m<sup>2</sup> (Denic et al., 2014; Pander et al., 2015). In addition, changes of flow regimes can facilitate deposition of fines and degradation of spawning grounds (Auerswald & Geist, 2018).

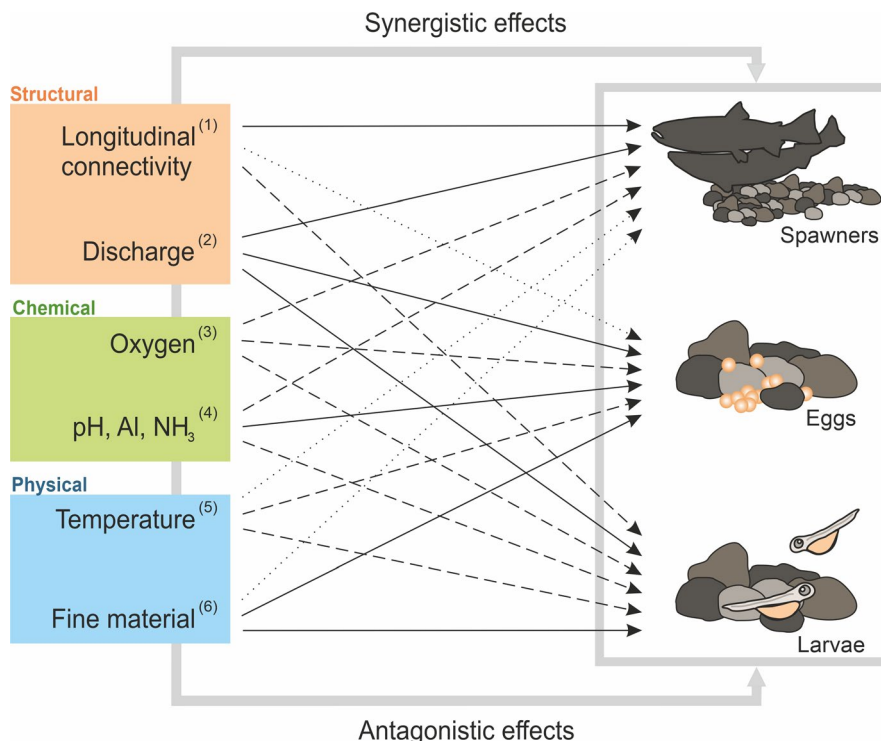
Accumulating fine material causes compaction and colmation of the river bed at spawning sites. Consequently, fish need more effort in relocating the strongly solidified substrate during redd cutting, which, under certain circumstances, may no longer be possible. Consequences include interrupted or completely lost spawning processes or superficially laid eggs, with a higher risk to drift away or being preyed upon (Crisp, 1990).

In evolutionary terms, Atlantic salmon and brown trout have adapted their spawning behaviour to natural deposition of fines by cutting a redd into the gravel, which cleans the substrate naturally from fines (Kondolf & Wolman, 1993). After egg deposition, new arriving fine material ideally continues to be removed by the current as the loosely backfilled gravel is permeable to a certain extent. However, in case of high fine material loads, the substrate can quickly colmate again. Since winter spawning salmonids have a long egg development time (up to five months) (Acornley & Sear, 1999; Mueller et al., 2014; Soulsby et al., 2001; Sternecker et al., 2014), it can happen that the gravel cleaned by the female prior to egg deposition does not remain so through the development time of the eggs. Eggs of other salmonids, such as grayling or Danube salmon, which are laid in spring (Northcote, 1995; Sternecker et al., 2014), develop faster due to the higher ambient water temperature and thus have a shorter exposure time (Sternecker et al., 2014).

Embryonic growth can be influenced both directly and indirectly by the complex interaction of interstitial permeability, oxygen availability, temperature and rising groundwater (Greig et al., 2007) by fine materials. Due to these complex interactions, most studies do not distinguish between the exact physical and chemical effects of fine materials on the success of egg development and emergence (Heywood & Walling, 2007; Malcolm et al., 2003a,b; Pander et al., 2009; Rubin, 1998; Witzel & MacCrimmon, 1983), but rather represent the overall survival rates in different fine material fractions (Mueller et al., 2014). However, there are two main processes that need to be considered. Sand fractions can lead to a superficial sealing of the river bed (Beschta & Jackson, 1979; Sternecker & Geist, 2010) and thus build a physical barrier at the boundary layer between open water and hyporheic zone (Everest et al., 1987). The colmation of this upper most layer is most important in determining exchange of water and matter between the two compartments of open water and interstitial habitat (Geist & Auerswald, 2007). Additionally, colmation can change the chemical composition of the interstitial water and foster oxygen depletion with negative effects on hatching and emergence success (Everest et al., 1987; Sternecker et al., 2013a; Sternecker & Geist, 2010). Other indirect, sublethal or lethal effects can be evoked by toxic chemicals (e.g. heavy metals, pesticides, pharmaceuticals) or nutrients potentially bound to the fines (Kemp et al., 2011). Fine material falling through the upper, coarser, gravel layers fills the spawning redd from the bottom up (Acornley & Sear, 1999; Einstein, 1968; Pander et al., 2015; Turnpenny & Williams, 1980). In such a case, shallower spawning redds can replenish faster, which was often observed after gravel bed restoration (e.g. gravel addition) (Mueller et al., 2014; Pander et al., 2015). Eggs laid near the surface laying in deeper spawning redds would have a buffer, and thus, the eggs and larvae would be less prone to suffocate (Everest et al., 1987).

Mortality rates for eggs caused by high loads of fine material in the hyporheic zone can reach 86% (Soulsby et al., 2001) and more (Mueller et al., 2014). Greig et al. (2005b) found that particles  $D < 4 \mu\text{m}$  can block the micro pores of the egg membrane and thus strongly impair the oxygen supply, which led to a weaker growth rate of the embryos. Larvae of brown trout and Atlantic salmon exposed to a high fine material rate had larger yolk sacs than the control group that was not exposed to fine material. Larvae with larger yolk sacs are poorer swimmers and therefore more susceptible to predators or drifting, because, due to their size, they are mostly located in larger-pored areas of the interstitial zone and thus mostly near the gravel surface (Louhi et al., 2011).

The larvae emerge from the sediment after absorption of their yolk sac and drift to shallow near-bank habitats. This necessary process is only possible if the larvae are able to ascend through the gravel gaps. Hence, sand-sized particles often hinder the emergence of larvae (Crisp, 1993; Hartman & Hakala, 2006; Kondolf, 2000; Sternecker & Geist, 2010). Furthermore, high loads of fine sediment may exert size-selective effects (Sternecker & Geist, 2010). In a laboratory experiment, Beschta and Jackson (1979) found that sand ( $D_{50} = 0.5 \text{ mm}$ ) tends to settle in the upper 10 cm of a stable gravel



**FIGURE 5** Risk scheme presenting levels of impact by six predominant environmental risks representing impacts acting on the structural, chemical and physical level in fresh water on the three critical life stages spawning, egg development and emergence of Atlantic salmon and brown trout. Displayed by arrows are also the individual effects of each risk on the three life stages: straight line = high negative impact, dashed line = medium negative impact, dotted line = low negative impact. Further, these risks can also act additively, synergistically and antagonistically. (1) The longitudinal connection is crucial for spawners to reach their spawning ground as they have a greater range of movement between habitats and during migration than stationary eggs and less mobile fry. (2) Discharge has a strong influence on all life stages. This is particularly true for spawners and fry, as it triggers natural processes such as the onset of spawning migration or the time of drift of emergent larvae. Furthermore, the runoff rate determines habitat features such as presence of riffle-pool structures, lentic areas or the persistence of redds during incubation important for Atlantic salmon and brown trout survival. (3) The temperature influence can be observed on multiple levels. It has direct effects on body condition (e.g. growth, metabolic rate, maturity), on food availability (e.g. plankton growth, hatching time) and the solubility of substances in water (e.g. oxygen, chemicals). Mobile life stages can change to other areas if ambient water temperature reaches unsuitable conditions. Eggs have a relatively high temperature tolerance and are more robust. However, they are directly affected by synergistic effects related to temperature. (4) A high oxygen availability is essential for the survival and successful development of Atlantic salmon and brown trout. Eggs are directly dependent on the local conditions in the hyporheic zone and thus more vulnerable to hypoxic events. (5) The shift of pH in water to more acid conditions has been a major problem in the 80s. Nowadays, a recovery from acidification in European waters is evident but may emerge again in light of climate change with increasing CO<sub>2</sub> concentrations (Evans et al., 2001; Skjelkvåle et al., 2003). Since a change in pH can lead to growth depression, sublethal effects in vital organs or high mortality rates in the early-life stages of salmonids (eggs and larvae) are considered more vulnerable than spawners. On the other hand, eutrophication resulting in high pH values and increased ammonia toxicity needs to be considered. (6) Fine material has a high impact on the permeability of the hyporheic zone, and therefore, high loads can have detrimental consequences for eggs and fry. Spawning individuals may need to put more energy into redd cutting, but the overall negative impact is comparatively low

bed and forms a physical barrier. Sternecker and Geist (2010) also found the same effect in their emergence experiment with brown trout at substrate sizes of 5–8 mm.

## 5 | CURRENT STATUS OF THREATS TO SALMONID POPULATIONS IN FRESH WATER

In addition to the already well-characterised threats in the marine environment, such as exploitation (ICES, 2019 a,b; NASCO, 2019),

disease and introduced parasites (e.g. *Gyrodactylus salaris* [Johnsen & Jenser, 1991] and salmon lice *Lepeophtheirus salmonis* [Thorstad et al., 2015]), as well as genetical mixing with escaped farmed salmon (Karlsson et al., 2016), this review highlights the importance of considering the early-life stages in fresh water for sustainable management of the populations of both *Salmo salar* and *Salmo trutta fario*.

The different threats described herein impact spawning, egg development and emergence of both species by acting on the structural, chemical and physical levels (Figure 5). The intensity and interactions of the different environmental variables also depend on whether they affect the critical life stages solely, additively,

synergistically or antagonistically (Figure 5). Based on this review, the environmental threats for Atlantic salmon and brown trout can be classified into three categories: (i) prominent threats from the past against which actions have been taken; (ii) long-known threats that have further accelerated and lack action; and (iii) emerging threats holding unknown consequences for the future.

## 5.1 | Prominent threats from the past

In the 1970s and 1980s, freshwater acidification was one of the major environmental threats to aquatic biota, especially in northern Europe and eastern North America in calcium-poor rivers where the buffering capacity of the ecosystems naturally is rather low (Overrein et al., 1980). Through the application of suitable mitigation measures (e.g. liming; Hultberg & Andersson, 1982) and introduction of new laws and regulations affecting the sources of acidifying gases (e.g. Convention on Long-range Transboundary Air Pollution in 1979; UN/ECE, 1999), freshwater systems across Europe are now slowly recovering (Evans et al., 2001; Geller & Schultze, 2009; Skjelkvåle et al., 2001; Stoddard et al., 1999). In the course of this recovery, it was also possible to re-establish lost Atlantic salmon and brown trout populations in previously acidified rivers (Degerman & Appelberg, 1992; Hesthagen et al., 2017; Howells et al., 1992). However, chemical and especially biological recovery can be costly and slow, and other threats (e.g. climate change, land-use practises, habitat degradation) may negatively affect the recovery process (Austnes et al., 2018; Skjelkvåle et al., 2003). Climate change, for instance, may bring back acidification through increased dissolution of carbonic acid in fresh water (Weiss et al., 2018).

## 5.2 | Long-known threats further accelerating

The negative impacts of missing longitudinal connectivity and habitat functionality due to structural deficits on riverine fish are well documented and continue to be the major challenge for the future of freshwater conservation (Geist, 2011, 2015; Grill et al., 2015; Grill et al., 2019). Analogously to other cold-water adapted species, access to cold-water patches and refugia during extended hot periods becomes a crucial factor of population resilience in the light of global warming (Kuhn et al., 2021). For Atlantic salmon and brown trout, both factors are considered key management objectives to re-establish self-sustainable populations in fresh water (Birnie-Gauvin et al., 2017; ICES, 2019a, 2019b, 2019c). On one hand, the difficulty is finding a compromise between river ecosystem conservation and human demands for green energy, flood protection, shipping routes and land use (Geist, 2021; Jackson, 2011; Poff et al., 2003). On the other hand, there is a lack of action for already existing solutions. While the implementation of the EU Water Framework Directive (WFD; 2000/60/EC) was meant to force action on the member states of Europe to improve the state of river ecosystems including connectivity, only 41% of all rivers in the European Union match the

formulated goal of a good ecological status (Kristensen et al., 2018). It is widely considered that the implementation of the respective management plans as a basis for the restoration of surface waters cannot meet the deadlines set by the EU to reach the goals of the WFD. More than two decades after implementation of the WFD, many experts claimed that these goals were "over-ambitious" resulting in several extensions of deadlines to match the good ecological status of surface waters (Hering et al., 2010).

Another remaining problem is the re-establishment of habitat functionality. Of key importance for the early-life stages of salmonids is the quality of the spawning ground, particularly the well-characterised problem of siltation and colmation of salmonid spawning sites through land use (agriculture, forestry, urban and industrial wastewater) resulting in egg and larval die offs. Now, this knowledge has been complemented by the observation that the problem of colmation can only be solved if combined with approaches of re-establishing flow regimes and mitigation of in-stream modifications of geomorphic structure through carbonate precipitation and internal biomass production (Auerswald & Geist, 2018; Geist & Hawkins, 2016). Some measures such as local, small-scale in-stream spawning site restorations (e.g. gravel supplementation or substrate loosening by raking, power hosing or excavation) seem quick, cheap and effective, but their effects often persist for less than one year, especially in catchments with intense agricultural and forest land use (Mueller et al., 2014; Pander et al., 2015; Sterneckner et al., 2013b). Hence, despite the economic investment, long history and volumes of literature, considerable uncertainties and controversial debates about the biological effectiveness of such measures remain (Birnie-Gauvin et al., 2019; Louhi et al., 2016; Mueller et al., 2014; Pander & Geist, 2016; Roni et al., 2015; Szałkiewicz et al., 2018; Vehanen et al., 2010b), causing delays in their implementation.

## 5.3 | Emerging threats

It should be acknowledged that many European countries made great progress in reducing chemical pollution and nutrient inputs to freshwater ecosystems in the past 30 years. The implementation of a tertiary phase in sewage water treatment as well as the replacement or reduction in chemicals and nutrients in industrial production, land use and household disposal significantly decreased loads of nitrate, phosphate and airborne acidification (Geist & Hawkins, 2016). In addition, laws and regulations have been implemented to further improve the ecological status of surface waters in all European countries, including threshold limits for specific priority substances and nutrient loads (WFD; 2000/60/EC). While the overall chemical and nutrient status of European surface waters is slowly recovering, some countries (e.g. England, Germany, Sweden) are currently failing to meet the limits, largely due to agricultural inputs (e.g. pesticides, fertilisers; Kristensen et al., 2018).

There are many chemicals of which the effects on the early-life stages of Atlantic salmon and brown trout are not well understood. There are arguably three main reasons. The first is that most research



on the effects of chemicals on biologic systems is conducted on one specific chemical of interest at a time, while in the real-world most organisms are exposed to mixtures of multiple chemicals at the same time. There can be additive or non-additive, synergistic or antagonistic effects, sometimes also referred to as “cocktail effects” (Connon et al., 2012). The second reason is that most studies tend to focus on acute (i.e. short-term) effects, whereas more realistic chronic exposure scenarios can have cumulative detrimental consequences for organisms (Spromberg & Meador, 2005). The third reason is that the bioavailability of substances in reality may differ from test results of standard toxicity testing (Beggel et al., 2010). Generally, the young life stages tend to be more susceptible to negative effects than adult fish, but chronic exposure and potential cumulative effects of especially persistent chemicals can also affect reproductive output (Mohammed, 2013). An effect assessment is further complicated by the effects of these chemicals on the entire food web (Malaj et al., 2014). Insecticides may be particularly harmful to non-target species, including terrestrial and freshwater insects, which both can make an important contribution to the diet of brown trout and Atlantic salmon during their freshwater life stages.

Another threat becoming increasingly prominent during the last decade is climate change (for review see Harrod et al., 2009; Jonsson & Jonsson, 2009). The most likely scenarios for the main distribution areas of Atlantic salmon and brown trout include higher temperatures, wetter winters, dryer summers and more extreme events of flooding and drought (ICES, 2017b; IPCC, 2007, 2014) affecting all components of the freshwater ecosystem (Wilby et al., 2006). Models and predictions of the consequences of climate change have focussed on the adaptability of Atlantic salmon and brown trout to rising temperatures during different life stages (Casas-Mulet et al., 2020; Sternecker et al., 2014). The likelihood for future losses of salmonid populations is considered high, especially in their lower latitude distribution range. However, there is still a lack of knowledge on the extent of climate change impacts (Jonsson & Jonsson, 2009; Skjelkvåle et al., 2003) and the possible interaction with existing or emerging stressors. For example, extreme climatic events (drought followed by extreme rainfall) in combination with changed flow regimes (e.g. hydropower) and erosion-prone land use can lead to higher loads of fine material and nutrients being washed into the waterbody. The combination of all or some of these factors will most likely result in unfavourable conditions for egg development and subsequent recruitment. Gregory et al. (2020) found that the 2016 salmon recruitment crash in Wales was most likely caused by the unfavourable combination of warm spawning temperatures, which can inhibit spawning, and higher flood frequencies during egg incubation and emergence, resulting in washouts of eggs and alevins. Such inclement conditions could become more common under future climate change. The predicted increase in the average temperature in the next years is suspected to facilitate the spread of parasites (Bruneaux et al., 2017), invasive species (Bean, 2020) and increase the toxic effects of pollutants (Dar et al., 2020) with negative consequences for all life stages of Atlantic salmon and brown trout. From the perspective of research and management, it is thus

particularly important to (i) understand and predict the effects of climate change on habitat suitability for both species; (ii) identify and ensure access to cold-water refugia as a key to improving population resilience (Kuhn et al., 2021); and (iii) understand and manage the interactions with other stressors, especially those that are also temperature dependent.

In addition to these large-scale impacts, local biological interactions following (re-) introductions of species that interact with the life cycles of Atlantic salmon and brown trout must be considered. This includes stocking with non-native rainbow trout as well as (re-) introductions of ecosystem engineers such as beavers, for which effects remain controversial. In contrast to the potential structural enrichment of stream habitats by beavers, their reintroduction is sometimes also seen as an emerging threat to salmonid populations as beaver activities (i.e. the creation of dams) generally have the potential to impair fish migration and alter spawning grounds. For example, Mitchell and Cunjak (2007) suggested that the cumulative effect of several beaver dams may have reduced salmon movements and spawning upstream the obstacles in Canadian streams in some years. By contrast, Parker and Rønning (2007) concluded in their Norwegian study that the presence of beavers is likely to have an insignificant negative impact on the reproduction of salmonids. Further, a review of beaver activity impacts on fish populations by Collen and Gibson (2001) suggested more positive than negative impacts, but the size of the stream should be considered as well as the location of the beaver activity and size of the dams constructed. In small, narrow streams beaver activity can have a greater influence on habitat quality and fish communities as these streams get more easily dammed (Rosell et al., 2005). Hence, more research is needed to monitor possible consequences of beaver reintroduction on salmonid populations.

## 5.4 | Cumulative effects

Although all threats have been described individually in their effects on the critical life stages of Atlantic salmon and brown trout (Figure 5), it is important to highlight that it is their diversity and complexity combined with these stressors often acting in concert and in a non-linear way, which complicates a mechanistic understanding of their exact modes of action as well as a translation into effective mitigation measures (Armstrong et al., 1998; Bierschenk et al., 2019; Mueller et al., 2020; Mueller et al., 2017; Ormerod et al., 2010). The complex interactions between the stressors are not yet fully understood but are increasingly being addressed (e.g. Brook et al., 2008; Jackson et al., 2015; Bouraï et al., 2020).

There is also increasing evidence of negative indirect effects of stressors on fish. For example, when pollutants exert direct effects on keystone species or induce changes in nutrient and oxygen dynamics, they may alter ecosystem functions essential for the critical life stages of Atlantic salmon and brown trout (Fleeger et al., 2003). Nutrient enrichment (eutrophication) and rise in water temperature act additively and can influence fish community

dynamics (Jackson et al., 2015; Bouraï et al., 2020). A meta-analysis conducted on net effects of cumulative impacts of multiple stressors (novel and extreme environmental changes) in freshwater ecosystems by Jackson et al. (2015) revealed that the net effects of stressor pairs were frequently more antagonistic (41%) than synergistic (28%), additive (16%) or reversed (15%). Furthermore, they suggested that “a possible explanation for the more antagonistic responses of freshwater biota to stressors is that the inherently greater environmental variability of smaller aquatic ecosystems promotes a greater potential for acclimatisation and co-adaptation to multiple stressors.”

## 6 | IMPLICATIONS FOR RESEARCH AND MANAGEMENT

Despite some uncertainties related to the emerging threats, the current knowledge of Atlantic salmon and brown trout is considered sufficient to mitigate current environmental risks in a way that populations could quickly recover their strength (Lobón-Cerviá, 2009) and increase their general resilience against stressors. For long-lasting solutions, a “stopping at the source” strategy is considered most promising. This includes river restoration measures to re-establishing connectivity and improve habitat quality in particular as these threats have the greatest impact on all life stages today (Dudgeon, 2019; Figure 5), and as they are particularly crucial in the light of climate change increasing the relevance of access to cold-water patches and minimising combined effects of temperature and fines on interstitial habitats important for egg development. There is strong evidence that with approximately one barrier every two kilometres of river, Europe has the most fragmented rivers in the world (AMBER, 2020; Grill et al., 2019). Yet, 13% of these barriers are obsolete obstacles (approx. 156,000), which do not serve any purpose and could be removed. Dam removals can have an extremely positive influence on the abundance of salmonid species (Birnie-Gauvin et al., 2017). Where obstacle removal is not possible, measures to restore fish migration by considering the individual requirements of species (e.g. water depth, discharge, behaviour) should be obligatory (Silva et al., 2018).

Further, there is no way around an appropriate adjustment of land use in terms of a selection of low erosion cultivation methods, crop rotation and suitable cultivation strategies at the catchment scale. In addition, buffer strips and field wetlands can be a promising mitigation measure not only preventing diffuse input of sediments and associated pollutants into fresh waters, which directly affect processes relevant for early-life stages of salmonids (Knott et al., 2019; Ockenden et al., 2012), but also enhancing biodiversity and aesthetics (Barling & Moore, 1994; Cole et al., 2020). Up to now, fine sediment input in surface waters is a key factor affecting trout and salmon from spawning to emergence but is barely considered in WFD monitoring, which should implement a new standard for the monitoring of fine sediment input in surface waters as soon as possible.

The WFD has already set limits for nutrient and chemical inputs into fresh waters, but most European countries have not complied with these standards (Brack et al., 2019). More regular controls and stricter penalties for non-compliance could improve the situation. In addition, scientists from the EU-funded project “SOLUTIONS for present and future emerging pollutants in land and water resources management” (<https://www.solutions-project.eu>) call for an improvement of the WFD and current water laws through a more holistic approach of protection from and monitoring of chemical pollution. The status assessments should not only address the selected priority pollutants (currently set by the WFD), but all chemicals that pose a risk, as well as assessing mixture effects and considering mitigation options at an early stage of the assessment (Brack et al., 2019).

In addition to “stopping at the source,” some preventive actions can minimise the impact of some current and emerging threats. For example, Switzerland upgraded existing wastewater treatment plants to reduce micropollutants and toxicities from wastewater effluents (Eggen et al., 2014). Further, the reintroduction of more structures in habitats, shading vegetation and natural groundwater inflows would offer valuable thermal refugia for salmonid fish, which may help to counteract some of the negative effects of climate change (Kuhn et al., 2021).

Already established measures such as stocking can, properly applied, stabilise depressed populations. However, long-term stocking has often been associated with stocking different genetic backgrounds (Aas et al., 2018; Bernás & Wąs-Barcz, 2020; Finnegan & Stevens, 2008) and this can lead to negative genetic effects on extant populations when stocked and wild fish interbreed (e.g. Machordom et al., 1999; Nielsen et al., 2001; Marzano et al., 2003; McGinnity et al., 2003; Ferguson, 2006). This relates to both *Salmo salar* and *Salmo trutta fario*. Interbreeding of distant genetic lines can result in outbreeding depression or lowered survival in subsequent generations, as non-local stocks tend to have reduced survival rates compared with natural populations (McGinnity et al., 2003; Araki et al., 2008; Ågren et al., 2019). In addition, genetic mixing can result in the reduction of local adaptations (McGinnity et al., 1997; Wang et al., 2002; Bourret et al., 2011). *Salmo salar* in particular is known to exhibit distinctive adaptations to single rivers or catchments (Ikediashi et al., 2018; Ozerov et al., 2012; Verspoor, 1997) and is therefore particularly prone to loss of genetic diversity at the metapopulation level (Griffiths et al., 2010). Due to its popularity as a game fish, *Salmo trutta fario* has been introduced to rivers for fishing for example in New Zealand, India and South Africa (Aass, 1982). Stocked fish usually originate from hatcheries that are able to produce large numbers of juvenile Atlantic salmon and brown trout. Hence, hatcheries have a responsibility to develop stocks that more closely resemble wild stocks in their genetics and behaviour and only use appropriate close relative stocks in rebuilding Atlantic salmon and brown trout populations. This way unique stocks can be better conserved and protected. Before stocking, however, river restoration (improving water quality, river access and structure) should be prioritised (Ikediashi et al., 2012).



When mitigating freshwater threats, it is further necessary to take a holistic approach considering all environmental stressors connected to the health of the critical life stages of Atlantic salmon and brown trout (Calles & Greenberg, 2009; Pander & Geist, 2013; Tummers et al., 2016). Stocking of fish, for example, cannot support a local population if the migration rate or mortality rate due to unsuitable habitat conditions, turbine mortality, predation or disease exceed stock recruitment (Aarts et al., 2004; Cowx, 1994). Further, habitat restoration should consider the catchment scale and should include a functional perspective on hydrogeomorphic, biogeochemical and ecological processes that may significantly improve the understanding of in-stream processes and how threats affect habitats (Pander & Geist, 2016).

Despite a long research history on Atlantic salmon and brown trout, knowledge gaps on some autecological requirements and population development still exist, which should be addressed. This includes knowledge on minimum viable population size in different habitat types, general spatial requirements of all life stages, synergistic effects between environmental factors and physiological response, and short-term and long-term adaptability to rapid changing environmental conditions (Jonsson & Jonsson, 2011; Smialek et al., 2019). In contrast to physical habitat characteristics (e.g. current speed, sediment composition, water depth and oxygen levels), this information is difficult to obtain and depends on complex synergistic effects or sometimes unpredictable factors. In cases where data are missing for one species, it might be feasible to attribute findings from another well-studied species to its less studied related species to have a starting point for action. For Atlantic salmon and brown trout, the habitat requirements and their sensitivities to the environmental risks during the three critical life stages spawning, egg development and emergence discussed are almost identical, creating synergies in conservation and restoration. This is mainly due to similarities in their spawning behavior (e.g. gravel spawners) and morphology (e.g. body shape, overlapping range in size spectrum). This is also underlined by both species being found together in key habitats, such as spawning grounds with the same hydromorphological characteristics, where they may hybridise with each other (Matthews et al., 2000; Youngson et al., 1992). Differences in the choice of habitat between Atlantic salmon and brown trout are only found to a limited extent and can essentially be attributed to two factors: (i) the overall size spectrum of both species; and (ii) the different life strategy after the juvenile stage. Hence, mitigation measures undertaken for Atlantic salmon will most likely be profitable for brown trout and vice versa.

## 7 | CONCLUSIONS

It is important to emphasise that improving freshwater conditions for the early-life stages of both species is essential in securing population resilience yet can only contribute in part to their conservation. As mentioned earlier, especially seaward-migrating forms are exposed to further stressors at sea (e.g. overfishing, sea lice

infestation, interbreeding with escaped farmed salmon) at a later stage of their life cycle. However, improving the starting conditions for these individuals (i.e. good conditions for early-life stages in fresh water) can also greatly improve their resilience in the later life stages (e.g. sending the healthiest smolts to sea) and their chance to face future risks with fewer losses. Furthermore, Atlantic salmon and brown trout inherit an admirable degree of adaptation themselves. The great plasticity in their life strategies is one key factor to their survival, and thus, it is important to protect this plasticity by conserving the genetical diversity between stocks.

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## REFERENCES

- Aarestrup, K. & Koed, A. (2003) Survival of migrating sea trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*) smolts negotiating weirs in small Danish rivers. *Ecology of Freshwater Fish*, 12, 169–176. <https://doi.org/10.1034/j.1600-0633.2003.00027.x>
- Aarts, B.G., Van Den Brink, F.W. & Nienhuis, P.H. (2004) Habitat loss as the main cause of the slow recovery of fish faunas of regulated large rivers in Europe: the transversal floodplain gradient. *River Research and Applications*, 20, 3–23. <https://doi.org/10.1002/rra.720>
- Aas, Ø., Cucherousset, J., Fleming, I.A., Wolter, C., Höjesjö, J., Buoro, M. et al. (2018) Salmonid stocking in five North Atlantic jurisdictions: identifying drivers and barriers to policy change. *Aquatic Conservation*, 28, 1451–1464. <https://doi.org/10.1002/aqc.2984>
- Aass, P. (1982). *Brown trout stocking in Norway*. Proceedings of the Symposium on Stock Enhancement in the Management of Freshwater Fisheries, held in conjunction with the Twelfth Session of EIFAC (Budapest Hungary, 31 May–2 June 1982). EIFAC Technical Paper, 42(1). Available at: <http://www.fao.org/3/ae996b/AE996B12.htm#ch11>. [Accessed 12th Dec 2020].
- Acornley, R.M. & Sear, D.A. (1999) Sediment transport and siltation of brown trout (*Salmo trutta* L.) spawning gravels in chalk streams. *Hydrological Processes*, 13, 447–458.
- Ågren, A., Vainikka, A., Janhunen, M., Hyvärinen, P., Piironen, J. & Kortet, R. (2019) Experimental crossbreeding reveals strain-specific variation in mortality, growth and personality in the brown trout (*Salmo trutta*). *Scientific Reports*, 9, 1–11. <https://doi.org/10.1038/s41598-018-35794-6>
- Alabaster, J.S. & Lloyd, R. (1982) *Water quality for freshwater fish*, 2nd edition. London: Butterworths.
- Alabaster, J.S., Shurben, D.G. & Knowles, G. (1979) The effect of dissolved oxygen and salinity on the toxicity of ammonia to smolts of salmon, *Salmo salar* L. *Journal of Fish Biology*, 15, 705–712. <https://doi.org/10.1111/j.1095-8649.1979.tb03680.x>
- AMBER. (2020). *European Barrier Atlas*. [Interactive map]. Available at: <https://amber.international/european-barrier-atlas/>
- Araki, H., Berejikian, B.A., Ford, M.J. & Blouin, M.S. (2008) Fitness of hatchery-reared salmonids in the wild. *Evolutionary Applications*, 1, 342–355. <https://doi.org/10.1111/j.1752-4571.2008.00026.x>

- Arevalo, E., Panserat, S., Seiliez, I., Larrañaga, A. & Bardonnat, A. (2018) Effect of food shortage and temperature on age 0+ salmonids: a contribution to predict the effects of climate change. *Journal of Fish Biology*, 92, 642–652. <https://doi.org/10.1111/jfb.13533>
- Arias, P., Pinochet, L.F. & Disi, A. (2002) Study of the nervous tissue development in rainbow trout (*Oncorhynchus mykiss*) embryos treated with oxytetracycline. *Anatomia, Histologia, Embryologia*, 31, 144–147. <https://doi.org/10.1046/j.1439-0264.2002.00376.x>
- Armstrong, J.D., Grant, J.W.A., Forsgren, H.L., Fausch, K.D., DeGraaf, R.M., Fleming, I.A. et al. (1998) The application of science to the management of Atlantic salmon (*Salmo salar*): integration across scales. *Canadian Journal of Fisheries and Aquatic Sciences*, 55, 303–311. <https://doi.org/10.1139/d98-014>
- Armstrong, J.D., Kemp, P.S., Kennedy, G.J.A., Ladle, M. & Milner, N.J. (2003) Habitat requirement of Atlantic salmon and brown trout in rivers and streams. *Fisheries Research*, 62, 143–170.
- Atse, C.B., Audet, C. & De La Noüe, J. (2002) Effects of temperature and salinity on the reproductive success of Arctic charr, *Salvelinus alpinus* (L.): egg composition, milt characteristics and fry survival. *Aquaculture Research*, 33, 299–309. <https://doi.org/10.1046/j.1355-557x.2002.00674.x>
- Auerswald, K. & Geist, J. (2018) Extent and causes of siltation in a headwater stream bed: catchment soil erosion is less important than internal stream processes. *Land Degradation & Development*, 29, 737–748. <https://doi.org/10.1002/ldr.2779>
- Aulstad, D. & Gjedrem, T. (1973) The egg size of salmon (*Salmo salar*) in Norwegian rivers. *Aquaculture*, 2, 337–341. [https://doi.org/10.1016/0044-8486\(73\)90166-X](https://doi.org/10.1016/0044-8486(73)90166-X)
- Austnes, K., Aherne, J., Arle, J., Čičendajeva, M., Couture, S., Fölster, J. et al. (2018). *Regional assessment of the current extent of acidification of surface waters in Europe and North America*. Report for the ICP Waters Report, Prepared at the ICP Waters Programme Centre Norwegian Institute for Water Research. Oslo, Norway, 136 pp. Available at: [http://pure.iiasa.ac.at/id/eprint/15542/1/ICPW\\_Report\\_135-2018.pdf](http://pure.iiasa.ac.at/id/eprint/15542/1/ICPW_Report_135-2018.pdf). [Accessed 12<sup>th</sup> Dec 2020].
- Baisez, A., Bach, J.M., Leon, C., Parouty, T., Terrade, R., Hoffmann, M. et al. (2011) Migration delays and mortality of adult Atlantic salmon *Salmo salar* en route to spawning grounds on the River Allier, France. *Endangered Species Research*, 15, 265–270. <https://doi.org/10.3354/esr00384>
- Banks, J.W. (1969) A review of the literature on the upstream migration of adult salmonids. *Journal of Fish Biology*, 1, 85–136. <https://doi.org/10.1111/j.1095-8649.1969.tb03847.x>
- Bardonnat, A. & Baglinière, J.L. (2000) Freshwater habitat of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, 57, 497–506. <https://doi.org/10.1139/f99-226>
- Bardonnat, A., Gaudin, P. & Thorpe, J.E. (1993) Diel rhythm of emergence and of first displacement downstream in trout (*Salmo trutta*), Atlantic salmon (*Salmo salar*) and grayling (*Thymallus thymallus*). *Journal of Fish Biology*, 43, 755–762. <https://doi.org/10.1111/j.1095-8649.1993.tb01152.x>
- Barlaup, B.T. & Åtland, Å. (1996) Episodic mortality of brown trout (*Salmo trutta* L.) caused by sea-salt-induced acidification in western Norway: effects on different life stages within three populations. *Canadian Journal of Fisheries and Aquatic Sciences*, 53, 1835–1843. <https://doi.org/10.1139/f96-108>
- Barlaup, B.T., Gabrielsen, S.E., Skoglund, H. & Wiers, T. (2008) Addition of spawning gravel—a means to restore spawning habitat of Atlantic salmon (*Salmo salar* L.), and anadromous and resident brown trout (*Salmo trutta* L.) in regulated rivers. *River Research and Applications*, 24, 543–550. <https://doi.org/10.1002/rra.1127>
- Barlaup, B.T., Lura, H., Sægrov, H. & Sundt, R.C. (1994) Inter- and intra-specific variability in female salmonid spawning behaviour. *Canadian Journal of Zoology*, 72, 636–642. <https://doi.org/10.1139/z94-086>
- Barling, R.D. & Moore, I.D. (1994) Role of buffer strips in management of waterway pollution: a review. *Journal of Environmental Management*, 18, 543–558. <https://doi.org/10.1007/BF02400858>
- Battini, M., Rocco, V., Lozada, M., Tartarotti, B. & Zagarese, H.E. (2000) Effects of ultraviolet radiation on the eggs of landlocked *Galaxias maculatus* (Galaxiidae, Pisces) in northwestern Patagonia. *Freshwater Biology*, 44, 547–552. <https://doi.org/10.1046/j.1365-2427.2000.00600.x>
- Bean, C.W. (2020) Atlantic salmon and non-native species: is there an issue? In: Thorstad, E.B., Bliss, D., Damon-Randall, K., Hanson, H., Horsburgh, G., Maoiléidigh, N.Ó., Sutton, S.G., Newton, V. & Hatfield, E.M.C. (Eds.) *Managing the Atlantic Salmon in a rapidly changing environment—management challenges and possible responses*. Tromsø: NASCO IYS Symposium, pp. 105–116.
- Beggel, S., Werner, I., Connon, R.E. & Geist, J.P. (2010) Sublethal toxicity of commercial insecticide formulations and their active ingredients to larval fathead minnow (*Pimephales promelas*). *Science of the Total Environment*, 408, 3169–3175. <https://doi.org/10.1016/j.scitotenv.2010.04.004>
- Belletti, B., Garcia de Leaniz, C., Jones, J., Bizzi, S., Börger, L., Segura, G. et al. (2010) More than one million barriers fragment Europe's rivers. *Nature*, 588, 436–441.
- Benejam, L., Saura-Mas, S., Bardina, M., Solà, C., Munné, A. & García-Berthou, E. (2016) Ecological impacts of small hydropower plants on headwater stream fish: from individual to community effects. *Ecology of Freshwater Fish*, 25, 295–306. <https://doi.org/10.1111/eff.12210>
- Berg, O.K. (1985) The formation of non-anadromous populations of Atlantic salmon, *Salmo salar* L., in Europe. *Journal of Fish Biology*, 27, 805–815. <https://doi.org/10.1111/j.1095-8649.1985.tb03222.x>
- Bergerot, B. & Cattaneo, F. (2017) Hydrological drivers of brown trout population dynamics in France. *Ecology*, 10, e1765. <https://doi.org/10.1002/eco.1765>
- Bergheim, A. & Hesthagen, T. (1990) Production of juvenile Atlantic salmon, *Salmo salar* L., and brown trout, *Salmo trutta* L., within different sections of a small enriched Norwegian river. *Journal of Fish Biology*, 36, 545–562. <https://doi.org/10.1111/j.1095-8649.1990.tb03556.x>
- Bernaś, R. & Wąs-Barcz, A. (2020) Genetic structure of important resident brown trout breeding lines in Poland. *Journal of Applied Genetics*, 61, 239–247. <https://doi.org/10.1007/s13353-020-00548-6>
- Beschta, R.L. & Jackson, W.L. (1979) The intrusion of fine sediments into a stable gravel bed. *Journal of the Fisheries Research Board Canada*, 36, 204–210. <https://doi.org/10.1139/f79-030>
- Bierschenk, A.M., Mueller, M., Pander, J. & Geist, J. (2019) Impact of catchment land use on fish community composition in the headwater areas of Elbe, Danube and Main. *Science of the Total Environment*, 652, 66–74. <https://doi.org/10.1016/j.scitotenv.2018.10.218>
- Bierschenk, B.M., Pander, J., Mueller, M. & Geist, J. (2018) Fish injury and mortality at pumping stations: a comparison of conventional and fish-friendly pumps. *Marine and Freshwater Research*, 70, 449–458. <https://doi.org/10.1071/MF18116>
- Bijlsma, R. & Loeschcke, V. (2012) Genetic erosion impedes adaptive responses to stressful environments. *Evolutionary Applications*, 5, 117–129. <https://doi.org/10.1111/j.1752-4571.2011.00214.x>
- Birnie-Gauvin, K., Franklin, P., Wilkes, M. & Aarestrup, K. (2019) Moving beyond fitting fish into equations: progressing the fish passage debate in the Anthropocene. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 29, 1095–1105. <https://doi.org/10.1002/aqc.2946>
- Birnie-Gauvin, K., Larsen, M.H., Nielsen, J. & Aarestrup, K. (2017) 30 years of data reveal dramatic increase in abundance of brown trout following the removal of a small hydrodam. *Journal of Environmental Management*, 204, 467–471. <https://doi.org/10.1016/j.jenvman.2017.09.022>



- Bishai, H.M. (1962) Reactions of larval and young salmonids to water of low oxygen concentration. *ICES Journal of Marine Science*, 27, 167–180. <https://doi.org/10.1093/icesjms/27.2.167>
- Boavida, I., Santos, J.M., Ferreira, T. & Pinheiro, A. (2015) Barbel habitat alterations due to hydropowering. *Journal of Hydro-environment Research*, 9, 237–247. <https://doi.org/10.1016/j.jher.2014.07.009>
- Bond, N. & Lake, P. (2003) Local habitat restoration in streams: constraints on the effectiveness of restoration for stream biota. *Ecological Management & Restoration*, 4, 193–198. <https://doi.org/10.1046/j.1442-8903.2003.00156.x>
- Booth, C.E., McDonald, D.G., Simons, B.P. & Wood, C.M. (1988) Effects of aluminium and low pH on net ion fluxes and ion balance in the brook trout (*Salvelinus fontinalis*). *Canadian Journal of Fisheries and Aquatic Sciences*, 45, 1563–1574. <https://doi.org/10.1139/f88-186>
- Bourai, L., Logez, M., Laplace-Treytore, C. & Argillier, C. (2020) How do eutrophication and temperature interact to shape the community structures of phytoplankton and fish in lakes? *Water*, 12, 779. <https://doi.org/10.3390/w12030779>
- Bourret, V., O'Reilly, P.T., Carr, J.W., Berg, P.R. & Bernatchez, L. (2011) Temporal change in genetic integrity suggests loss of local adaptation in a wild Atlantic salmon (*Salmo salar*) population following introgression by farmed escapees. *Heredity*, 106(3), 500–510.
- Brack, W., Ait-Aissa, S., Altenburger, R., Cousins, I., Dulio, V., Escher, B. et al. (2019) Let us empower the WFD to prevent risks of chemical pollution in European rivers and lakes. *Environmental Sciences Europe*, 31, 47. <https://doi.org/10.1186/s12302-019-0228-7>
- Brook, B.W., Sodhi, N.S. & Bradshaw, C.J.A. (2008) Synergies among extinction drivers under global change. *Trends in Ecology and Evolution*, 23, 453–460. <https://doi.org/10.1016/j.tree.2008.03.011>
- Brown, D.J.A. & Lynam, S. (1981) The effect of sodium and calcium concentrations on the hatching of eggs and the survival of the yolk sac fry of brown trout, *Salmo trutta* L. at low pH. *Journal of Fish Biology*, 19, 205–211. <https://doi.org/10.1111/j.1095-8649.1981.tb05824.x>
- Bruneaux, M., Visse, M., Gross, R., Pukk, L., Saks, L. & Vasemägi, A. (2017) Parasite infection and decreased thermal tolerance: impact of proliferative kidney disease on a wild salmonid fish in the context of climate change. *Functional Ecology*, 31, 216–226. <https://doi.org/10.1111/1365-2435.12701>
- Brunke, M. (1999) Colmation and depth filtration within streambeds: retention of particles in hyporheic interstices. *International Review of Hydrobiology*, 84, 99–117. <https://doi.org/10.1002/iroh.199900014>
- Bunn, S.E. & Arthington, A.H. (2002) Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management*, 30, 492–507. <https://doi.org/10.1007/s00267-002-2737-0>
- Butler, J.R., Radford, A., Riddington, G. & Laughton, R. (2009) Evaluating an ecosystem service provided by Atlantic salmon, sea trout and other fish species in the River Spey, Scotland: the economic impact of recreational rod fisheries. *Fisheries Research*, 96, 259–266. <https://doi.org/10.1016/j.fishres.2008.12.006>
- Cairns, J. Jr (1970) Ecological management problems caused by heated waste water discharge into the aquatic environment. *Journal of the American Water Resources Association*, 6, 868–878. <https://doi.org/10.1111/j.1752-1688.1970.tb01646.x>
- Calles, O. & Greenberg, L. (2009) Connectivity is a two-way street—the need for a holistic approach to fish passage problems in regulated rivers. *River Research and Applications*, 25, 1268–1286. <https://doi.org/10.1002/rra.1228>
- Çalta, M. (2002) Does brown trout (*Salmo trutta* L.) larval development retardation caused by short-term exposure to low pH and elevated aluminium concentration affect a second episode of toxicity? *Journal of Applied Ichthyology*, 18, 210–215. <https://doi.org/10.1046/j.1439-0426.2002.00350.x>
- Carrick, T.R. (1979) The effect of acid water on the hatching of salmonid eggs. *Journal of Fish Biology*, 14, 165–172. <https://doi.org/10.1111/j.1095-8649.1979.tb03506.x>
- Casas-Mulet, R., Pander, J., Ryu, D., Stewardson, M.J. & Geist, J. (2020) Unmanned Aerial Vehicle (UAV)-based Thermal Infra-Red (TIR) and optical imagery reveals multi-spatial scale controls of cold-water areas over a groundwater-dominated riverscape. *Frontiers in Environmental Science*, 8, 64. <https://doi.org/10.3389/fenvs.2020.00064>
- Casas-Mulet, R., Saltveit, S.J. & Alfredsen, K. (2015) The survival of Atlantic salmon (*Salmo salar*) eggs during dewatering in a river subjected to hydropowering. *River Research and Applications*, 31, 433–446. <https://doi.org/10.1002/rra.2827>
- Caudill, C.C., Daigle, W.R., Keefer, M.L., Boggs, C.T., Jepson, M.A., Burke, B.J. et al. (2007) Slow dam passage in adult Columbia River salmonids associated with unsuccessful migration: delayed negative effects of passage obstacles or condition-dependent mortality? *Canadian Journal of Fisheries and Aquatic Sciences*, 64, 979–995. <https://doi.org/10.1139/f07-065>
- Chapman, D.W. (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.
- Clark, E. (1998) *Microthermal habitats in British rivers*. Doctoral thesis. Exeter: University of Exeter.
- Clarke, D., Purvis, W.K. & Mee, D. (1991) Use of telemetric tracking to examine environmental influences on catch/effort indices. A case study of Atlantic salmon (*Salmo salar* L.) in the R. Tywi, S. Wales. In Cowx, I.G. (Ed.) *Catch effort sampling strategies: their application in freshwater fisheries management*. London: Blackwell, pp. 33–48.
- Cole, L.J., Stockan, J. & Helliwell, R. (2020) Managing riparian buffer strips to optimise ecosystem services: a review. *Agriculture, Ecosystems & Environment*, 296, 106891. <https://doi.org/10.1016/j.agee.2020.106891>
- Collen, P. & Gibson, R.J. (2001) The general ecology of beavers (*Castor* spp.), as related to their influence on stream ecosystems and riparian habitats, and the subsequent effects on fish—a review. *Reviews in Fish Biology and Fisheries*, 10, 439–461.
- Connon, R., Geist, J. & Werner, I. (2012) Effect-based tools for monitoring and predicting the ecotoxicological effects of chemicals in the aquatic environment. *Sensors*, 12, 12741–12771. <https://doi.org/10.3390/s120912741>
- Courchamp, F., Berce, L. & Gascoigne, J. (2008) *Allee effects in ecology and conservation*. Oxford: Oxford University Press.
- Cousins, K.L. & Jensen, J.O. (1994) The effects of temperature on external egg membranes in coho salmon (*Oncorhynchus kisutch*) and the occurrence of soft-shell disease. *Canadian Journal of Zoology*, 72, 1854–1857. <https://doi.org/10.1139/z94-251>
- Cowx, I. (1994) Stocking strategies. *Fisheries Management and Ecology*, 1, 15–30. <https://doi.org/10.1111/j.1365-2400.1970.tb00003.x>
- Cresser, M. & Edwards, A. (1987) *Acidification of freshwaters*. Cambridge: Cambridge University Press.
- Crisp, D.T. (1989) Some impacts of human activities on trout, *Salmo trutta*, populations. *Freshwater Biology*, 21, 21–33. <https://doi.org/10.1111/j.1365-2427.1989.tb01345.x>
- Crisp, D.T. (1990) Some effects of application of mechanical shock at varying stages of development upon the survival and hatching time of British salmonid eggs. *Hydrobiologia*, 194, 57–65. <https://doi.org/10.1007/BF00012112>
- Crisp, D.T. (1993) The environmental requirements of salmon and trout in fresh water. *Freshwater Forum*, 3, 176–202.
- Crisp, D.T. (1996) Environmental requirements of common riverine European salmonid fish species in fresh water with particular reference to physical and chemical aspects. *Hydrobiologia*, 323, 201–221. <https://doi.org/10.1007/BF0000784>
- Crisp, D.T. (2000) *Trout and salmon: ecology, conservation and rehabilitation*. Oxford: Wiley-Blackwell.
- Crisp, D.T. & Carling, P.A. (1989) Observations on siting, dimensions and structure of salmonid redds. *Journal of Fish Biology*, 34, 119–134. <https://doi.org/10.1111/j.1095-8649.1989.tb02962.x>

- Cuinat, R. & Bomassi, P. (1987) Evolution de la situation pour le saumon du bassin Loire-Allier, de 1979 à 1985. In: Thibault, M. & Billard, R. (Eds.) *La restauration des rivières à saumons*. Paris: INRA, pp. 39–51.
- Cushing, D.H. (1975) *Marine Ecology and Fisheries*. London: Cambridge University Press.
- Cushing, D.H. (1990) Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Advances in Marine Biology*, 26, 249–293.
- Czerkies, P., Brzuzan, P., Kordalski, K. & Luczynski, M. (2001) Critical partial pressures of oxygen causing precocious hatching in *Coregonus lavaretus* and *C. albula* embryos. *Aquaculture*, 196, 151–158.
- Dar, G.H., Bhat, R.A., Kamili, A.N., Chishti, M.Z., Qadri, H., Dar, R. & et al. (2020) Correlation between pollution trends of freshwater bodies and bacterial disease of fish fauna. In Qadri, H., Bhat, R.A., Mehmood, M.A. & Dar, G.H. (Eds.) *Fresh water pollution dynamics and remediation* (pp. 51–67). Singapore: Springer. [https://doi.org/10.1007/978-981-13-8277-2\\_4](https://doi.org/10.1007/978-981-13-8277-2_4)
- Davidson, J.G., Eikås, L., Hedger, R.D., Thorstad, E.B., Rønning, L., Sjørven, A.D. et al. (2020) Migration and habitat use of the land-locked riverine Atlantic salmon *Salmo salar* småblank. *Hydrobiologia*, 847, 2295–2306. <https://doi.org/10.1007/s10750-020-04254-6>
- Davidson, J.G., Rikardsen, A.H., Thorstad, E.B., Halttunen, E., Mitamura, H., Præbel, K. et al. (2013) Homing behaviour of Atlantic salmon (*Salmo salar*) during final phase of marine migration and river entry. *Canadian Journal of Fisheries and Aquatic Sciences*, 70, 794–802. <https://doi.org/10.1139/cjfas-2012-0352>
- Daye, P.G. & Garside, E.T. (1979) Development and survival of embryos and alevins of the Atlantic salmon, *Salmo salar* L., continuously exposed to acidic levels of pH, from fertilization. *Canadian Journal of Zoology*, 57, 1713–1718. <https://doi.org/10.1139/z79-222>
- Daye, P.G. & Garside, E.T. (1980) Structural alterations in embryos and alevins of the Atlantic salmon, *Salmo salar* L., induced by continuous or short-term exposure to acidic levels of pH. *Canadian Journal of Zoology*, 58, 27–43. <https://doi.org/10.1139/z80-004>
- Degerman, E. & Appelberg, M. (1992) The response of stream-dwelling fish to liming. *Environmental Pollution*, 78, 149–155.
- Denic, M. & Geist, J. (2010) Habitat suitability analysis for lacustrine brown trout (*Salmo trutta*) in Lake Walchensee, Germany: implications for the conservation of an endangered flagship species. *Aquatic Conservation*, 20, 9–17. <https://doi.org/10.1002/aqc.1058>
- Denic, M., Stoeckl, K., Gum, B. & Geist, J. (2014) Physicochemical assessment of *Unio crassus* habitat quality in a small upland stream and implications for conservation. *Hydrobiologia*, 735, 111–122. <https://doi.org/10.1007/s10750-013-1467-z>
- Dirksmeyer, J. (2008) *Untersuchungen zur Ökomorphologie der Laichhabitate von Lachsen und Meerforellen in Deutschland*. Doctoral thesis. Solingen: University Cologne.
- Doadrio, I. (2001) *Atlas y libro rojo de los peces continentales de España*. Madrid: Ministerio de Medio Ambiente, pp. 376.
- Dudgeon, D. (2019) Multiple threats imperil freshwater biodiversity in the anthropocene. *Current Biology*, 29, 960–967. <https://doi.org/10.1016/j.cub.2019.08.002>
- Duerregger, A., Pander, J., Palt, M., Mueller, M., Nagel, C. & Geist, J. (2018) The importance of stream interstitial conditions for the early-life-stage development of the European nase (*Chondrostoma nasus* L.). *Ecology of Freshwater Fish*, 27, 920–932. <https://doi.org/10.1111/eff.12403>
- DWA. (2014) *Merkblatt DWA-M 509 Fischaufstiegsanlagen und fischpassierbare Bauwerke-Gestaltung, Bemessung, Qualitätssicherung*. Hennef: Deutsche Vereinigung für Wasserwirtschaft, Abwasser und Abfall e.V.
- Dynesius, M. & Nilsson, C. (1994) Fragmentation and flow regulation of river systems in the northern 3rd of the world. *Science*, 266, 753–762. <https://doi.org/10.1126/science.266.5186.753>
- Eggen, R.I., Hollender, J., Joss, A., Schärer, M. & Stamm, C. (2014) Reducing the discharge of micropollutants in the aquatic environment: the benefits of upgrading wastewater treatment plants. *Environmental Science and Technology*, 48, 7683–7689. <https://doi.org/10.1021/es500907n>
- EIFAC. (1969) Water quality criteria for European freshwater fish—water temperature and inland fisheries. *Water Research*, 3, 645–662. [https://doi.org/10.1016/0043-1354\(69\)90009-8](https://doi.org/10.1016/0043-1354(69)90009-8).
- Einstein, H.A. (1968) Deposition of suspended particles in a gravel bed. *Journal of Hydraulic Engineering*, 94, 1197–1205.
- Einum, S. & Fleming, I.A. (2000) Selection against late emergence and small offspring in Atlantic salmon (*Salmo salar*). *Evolution*, 54, 628–639. <https://doi.org/10.1111/j.0014-3820.2000.tb00064.x>
- Eklöv, A.G., Greenberg, L.A., Brönmark, C., Larsson, P. & Berglund, O. (1999) Influence of water quality, habitat and species richness on brown trout populations. *Journal of Fish Biology*, 54, 33–43. <https://doi.org/10.1111/j.1095-8649.1999.tb00610.x>
- Ellender, B.R., Rivers-Moore, N.A., Coppinger, C.R., Bellingan, T.A. & Weyl, O.L.F. (2016) Towards using thermal stress thresholds to predict salmonid invasion potential. *Biological Invasions*, 18, 3513–3525. <https://doi.org/10.1007/s10530-016-1244-9>
- Elliott, J.M. (1976) The downstream drifting of eggs of brown trout (*Salmo trutta* L.). *Journal of Fish Biology*, 9, 45–50. <https://doi.org/10.1111/j.1095-8649.1976.tb04660.x>
- Elliott, J.M. (1981) Some aspects of thermal stress on fresh-water teleosts. In: Pickering, A.D. (Ed.) *Stress and fish*. London: Academic Press, pp. 43–50.
- Elliott, J.M. (1989) Wild brown trout *Salmo trutta*: an important national and international resource. *Freshwater Biology*, 21, 1–5. <https://doi.org/10.1111/j.1365-2427.1989.tb01343.x>
- Elliott, J.M. (1994) *Quantitative ecology and the brown trout*. Oxford: Oxford University Press.
- Elliott, J. & Elliott, J.A. (2010) Temperature requirements of Atlantic salmon *Salmo salar*, brown trout *Salmo trutta* and Arctic charr *Salvelinus alpinus*: predicting the effects of climate change. *Journal of Fish Biology*, 77, 1793–1817. <https://doi.org/10.1111/j.1095-8649.2010.02762.x>
- Environment Canada and Health Canada. (2001) *Canadian Environmental Protection Act CEPA 1999 - Priority Substances List Assessment Report - Ammonia in the Aquatic Environment*. Report for the Minister of Public Works and Government Services, Canada, 96 pp. Available at: <https://www.canada.ca/en/health-canada/services/environmental-workplace-health/reports-publications/environmental-contaminants/canadian-environmental-protection-act-1999-priority-substances-list-assessment-report-ammonia-aquatic-environment.html>. [Accessed 10th July 2020].
- EPA (United States Environmental Protection Agency). (2019) *National Recommended Water Quality Criteria - Aquatic Life Criteria Table*. Available at: <https://www.epa.gov/wqc/national-recommended-water-quality-criteria-aquatic-life-criteria-table>. [Accessed 18th June 2020].
- Eriksson, E. (1981) Aluminium in groundwater possible solution equilibria. *Hydrology Research*, 12, 43–50. <https://doi.org/10.2166/nh.1981.0004>
- Erkinaro, J., Økland, F., Moen, K., Niemelä, E. & Rahiala, M. (1999) Return migration of Atlantic salmon in the River Tana: the role of environmental factors. *Journal of Fish Biology*, 55, 506–516. <https://doi.org/10.1111/j.1095-8649.1999.tb00695.x>
- Essington, T.E., Sorensen, P.W. & Paron, D.G. (1998) High rate of redd superimposition by brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) in a Minnesota stream cannot be explained by habitat availability alone. *Canadian Journal of Fisheries and Aquatic Sciences*, 55, 2310–2316. <https://doi.org/10.1139/f98-109>
- EU (European Union). (1978) Directive 78/659/EEC of the European Parliament and of the Council of 18 July 1978 on the quality of fresh waters needing protection or improvement in order to support fish life. *Official Journal of the European Communities*, L222, 1–10.
- EU (European Union). (2000) Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing



- a framework for community action in the field of water policy. *Official Journal of the European Communities*, L327, 1–84.
- EU (European Union). (2006) Directive 2006/44/EC of the European Parliament and of the Council of 6 September 2006 on the quality of fresh waters needing protection or improvement in order to support fish life. *Official Journal of the European Union*, L264, 1–12.
- EUMOFA. (2019) *The EU fish market*. Luxembourg: Publications Office of the European Union, pp. 107. <https://doi.org/10.2771/168390>.
- Evans, C.D., Cullen, J.M., Alewell, C., Kopáček, J., Marchetto, A., Moldan, F. et al. (2001) Recovery from acidification in European surface waters. *Hydrology and Earth System Sciences*, 5, 283–298.
- Everest, F.H., Beschta, R.L., Scrivener, J.C., Koski, K.V., Sedell, J.R. & Cederholm, C.J. (1987) Fine sediment and salmonid production: a paradox. In: Salo, E.O. & Cundy, T.W. (Eds.) *Streamside management and forestry and fishery interactions*. Washington: College of Forest Resources University of Washington, pp. 89–142.
- Exley, C.A., Chappell, J.S. & Birchall, J.D. (1991) A mechanism for acute aluminium toxicity in fish. *Journal of Theoretical Biology*, 151, 417–427.
- Ferguson, A. (2006) *Genetic impacts of stocking on indigenous brown trout populations*. Environment Agency Science Report SC040071/SR. Bristol: Environment Agency, pp. 96.
- Finn, R.N. (2007) The physiology and toxicology of salmonid eggs and larvae in relation to water quality criteria. *Aquatic Toxicology*, 81, 337–354. <https://doi.org/10.1016/j.aquatox.2006.12.021>
- Finnegan, A.K. & Stevens, J.R. (2008) Assessing the long-term genetic impact of historical stocking events on contemporary populations of Atlantic salmon, *Salmo salar*. *Fisheries Management and Ecology*, 15, 315–326. <https://doi.org/10.1111/j.1365-2400.2008.00616.x>
- Finstad, A.G., Økland, F., Thorstad, E.B. & Heggberget, T.G. (2005) Comparing upriver spawning migration of Atlantic salmon *Salmo salar* and sea trout *Salmo trutta*. *Journal of Fish Biology*, 67, 919–930. <https://doi.org/10.1111/j.0022-1112.2005.00792.x>
- Fivelstad, S., Kallevik, H., Iversen, H.M., Møretrø, T., Våge, K. & Binde, M. (1993) Sublethal effects of ammonia in soft water on Atlantic salmon smolts at a low temperature. *Aquaculture International*, 1, 157–169. <https://doi.org/10.1007/BF00692618>
- Fleeger, J.W., Carman, K.R. & Nisbet, R.M. (2003) Indirect effects of contaminants in aquatic ecosystems. *Science of the Total Environment*, 317, 207–233.
- Forseth, T., Barlaup, B.T., Finstad, B., Fiske, P., Gjøsæter, H., Falkegård, M. et al. (2017) The major threats to Atlantic salmon in Norway. *ICES Journal of Marine Science*, 74, 1496–1513. <https://doi.org/10.1093/icesjms/fsx020>
- Freyhof, J. (2011). *Salmo trutta*. The IUCN Red List of Threatened Species 2011: e.T19861A9050312. Available at: <https://www.iucnredlist.org/species/19861/9050312>. <https://doi.org/10.2305/IUCN.UK.2008.RLTS.T19861A9050312.en>
- Freyhof, J. (2014). *Salmo salar*. The IUCN Red List of Threatened Species 2014: e.T19855A2532398. Available at: <https://www.iucnredlist.org/species/19855/9026693>. <https://doi.org/10.2305/IUCN.UK.1996.RLTS.T19855A9026693.en>
- García-Vázquez, E., Moran, P., Martínez, J.L., Pérez, J., De Gaudemar, B. & Beall, E. (2001) Alternative mating strategies in Atlantic salmon and brown trout. *Journal of Heredity*, 92, 146–149. <https://doi.org/10.1093/jhered/92.2.146>
- Garside, E.T. (1973) Ultimate upper lethal temperature of Atlantic salmon *Salmo salar* L. *Canadian Journal of Zoology*, 51, 898–900. <https://doi.org/10.1139/z73-135>
- Gaywood, M.J. (2018) Reintroducing the Eurasian beaver *Castor fiber* to Scotland. *Mammal Review*, 48, 48–61. <https://doi.org/10.1111/mam.12113>
- Geist, J. (2011) Integrative freshwater ecology and biodiversity conservation. *Ecological Indicators*, 11, 1507–1516. <https://doi.org/10.1016/j.ecolind.2011.04.002>
- Geist, J. (2015) Seven steps towards improving freshwater conservation. *Aquatic Conservation*, 25, 447–453. <https://doi.org/10.1002/aqc.2576>
- Geist, J. (2021) Green or red: challenges for fish and freshwater biodiversity conservation related to hydropower. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 31, 1551–1558.
- Geist, J. & Auerswald, K. (2007) Physicochemical stream bed characteristics and recruitment of the freshwater pearl mussel (*Margaritifera margaritifera*). *Freshwater Biology*, 52, 2299–2316. <https://doi.org/10.1111/j.1365-2427.2007.01812.x>
- Geist, J. & Hawkins, S.J. (2016) Habitat recovery and restoration in aquatic ecosystems: current progress and future challenges. *Aquatic Conservation*, 26, 942–962. <https://doi.org/10.1002/aqc.2702>
- Geist, J., Porkka, M. & Kuehn, R. (2006) The status of host fish populations and fish species richness in European freshwater pearl mussel (*Margaritifera margaritifera* L.) streams. *Aquatic Conservation*, 16, 251–266. <https://doi.org/10.1002/aqc.721>
- Geller, W. & Schultze, M. (2009) Acidification. In: Likens, G.E. (Ed.) *Encyclopedia of inland waters*. Oxford: Elsevier, pp. 1–12. <https://doi.org/10.1016/B978-012370626-3.00230-1>
- Gensemer, R.W. & Playle, R.C. (1999) The bioavailability and toxicity of aluminium in aquatic environments. *Critical Reviews in Environmental Science and Technology*, 29, 315–450. <https://doi.org/10.1080/10643389991259245>
- Gerlier, M. & Roche, P. (1998) A radio telemetry study of the migration of Atlantic salmon (*Salmo salar* L.) and sea trout (*Salmo trutta trutta* L.) in the upper Rhine. *Hydrobiologia*, 371, 283–293. <https://doi.org/10.1023/A:1017061608281>
- Gerstmeier, R. & Romig, T. (2003) *Die Süßwasserfische Europas*, 2nd edition. Stuttgart: Franckh-Kosmos Verlag GmbH & Co.
- Gibbins, C.N., Moir, H.J., Webb, J.H. & Soulsby, C. (2002) Assessing discharge use by spawning Atlantic salmon: a comparison of discharge electivity indices and PHABSIM simulations. *River Research and Applications*, 18, 383–395. <https://doi.org/10.1002/rra.685>
- Gibson, R.J. (1993) The Atlantic salmon in fresh water: spawning, rearing and production. *Reviews in Fish Biology and Fisheries*, 3, 39–73. <https://doi.org/10.1007/BF00043297>
- Gortázar, J., Alonso, C. & García de Jalón, D. (2012) Brown trout redd superimposition in relation to spawning habitat availability. *Ecology of Freshwater Fish*, 21, 283–292. <https://doi.org/10.1111/j.1600-0633.2011.00546.x>
- Gosset, C., Rives, J. & Labonne, J. (2006) Effect of habitat fragmentation on spawning migration of brown trout (*Salmo trutta* L.). *Ecology of Freshwater Fish*, 15, 247–254. <https://doi.org/10.1111/j.1600-0633.2006.00144.x>
- Gowans, A.R.D., Armstrong, J.D., Priede, I.G. & Mckelvey, S. (2003) Movements of Atlantic salmon migrating upstream through a fish-pass complex in Scotland. *Ecology of Freshwater Fish*, 12, 177–189. <https://doi.org/10.1034/j.1600-0633.2003.00018.x>
- Graham, C.T. & Harrod, C. (2009) Implications of climate change for the fishes of the British Isles. *Journal of Fish Biology*, 74, 1143–1205. <https://doi.org/10.1111/j.1095-8649.2009.02180.x>
- Grande, M., Muniz, I.P. & Andersen, S. (1978) Relative tolerance of some salmonids to acid waters. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, 20, 2076–2084. <https://doi.org/10.1080/03680770.1977.11896821>
- Gregory, S.D., Bewes, V.E., Davey, A.J., Roberts, D.E., Gough, P. & Davidson, I.C. (2020) Environmental conditions modify density-dependent salmonid recruitment: insights into the 2016 recruitment crash in Wales. *Freshwater Biology*, 65, 2135–2153. <https://doi.org/10.1111/fwb.13609>
- Gregory, S.D., Ibbotson, A.T., Riley, W.D., Nevoux, M., Lauridsen, R.B., Russell, I.C. et al. (2019) Atlantic salmon return rate increases with smolt length. *ICES Journal of Marine Science*, 76, 1702–1712. <https://doi.org/10.1093/icesjms/fsz066>

- Greig, S.M., Sear, D.A. & Carling, P.A. (2005a) The impact of fine sediment accumulation on the survival of incubating salmon progeny: implications for sediment management. *Science of the Total Environment*, 344, 241–258. <https://doi.org/10.1016/j.scitotenv.2005.02.010>
- Greig, S.M., Sear, D.A. & Carling, P.A. (2007) A review of factors influencing the availability of dissolved oxygen to incubating salmonid embryos. *Hydrological Processes*, 21, 323–334. <https://doi.org/10.1002/hyp.6188>
- Greig, S.M., Sear, D.A., Smallman, D. & Carling, P.A. (2005b) Impact of clay particles on the cutaneous exchange of oxygen across the chorion of Atlantic salmon eggs. *Journal of Fish Biology*, 66, 1681–1691. <https://doi.org/10.1111/j.0022-1112.2005.00715.x>
- Griffiths, A.M., Machado-Schiaffino, G., Dillane, E., Coughlan, J., Horreo, J.L., Bowkett, A.E. et al. (2010) Genetic stock identification of Atlantic salmon (*Salmo salar*) populations in the southern part of the European range. *BMC Genetics*, 11, 1–27.
- Grill, G., Lehner, B., Lumsdon, A.E., MacDonald, G.K., Zarfl, C. & Liermann, C.R. (2015) An index-based framework for assessing patterns and trends in river fragmentation and flow regulation by global dams at multiple scales. *Environmental Research Letters*, 10, 015001. <https://doi.org/10.1088/1748-9326/10/1/015001>
- Grill, G., Lehner, B., Thieme, M., Geenen, B., Tickner, D., Antonelli, F. et al. (2019) Mapping the world's free-flowing rivers. *Nature*, 569, 215–221. <https://doi.org/10.1038/s41586-019-1111-9>
- Gross, R., Nilsson, J. & Schmitz, M. (1996) A new species-specific nuclear DNA marker for identification of hybrids between Atlantic salmon and brown trout. *Journal of Fish Biology*, 49, 537–540. <https://doi.org/10.1111/j.1095-8649.1996.tb00049.x>
- Haag, J.J., White, J.S. & Logan, M. (2010). 2009 fish survey in recently dewatered western irrigation district canals. Prepared for: Western Irrigation District. Edmonton: AQUALITY Environmental Consulting Ltd.
- Hamor, T. & Garside, E.T. (1976) Developmental rates of embryos of Atlantic salmon, *Salmo salar* L., in response to various levels of temperature, dissolved oxygen, and water exchange. *Canadian Journal of Zoology*, 54, 1912–1917. <https://doi.org/10.1139/z76-221>
- Harby, A. & Noack, M. (2013) Rapid flow fluctuations and impacts on fish and the aquatic ecosystem. In: Maddock, I., Harby, A., Kemp, P. & Wood, P. (Eds.) *Ecohydraulics: an integrated approach*. Chichester: John Wiley & Sons Ltd, pp. 323.
- Harrod, C., Graham, C. & Mallela, J. (2009) Climate change and the fishes of Britain and Ireland. *Journal of Fish Biology*, 74, 1143–1205.
- Hartley, S.E. (1996) High incidence of Atlantic salmon x brown trout hybrids in a lake district stream. *Journal of Fish Biology*, 48, 151–154. <https://doi.org/10.1111/j.1095-8649.1996.tb01427.x>
- Hartman, K.J. & Hakala, J.P. (2006) Relationships between fine sediment and brook trout recruitment in forested headwater streams. *Journal of Freshwater Ecology*, 21, 215–230. <https://doi.org/10.1080/02705060.2006.9664990>
- Hastie, L. & Cosgrove, P. (2001) The decline of migratory salmonid stocks: a new threat to pearl mussels in Scotland. *Freshwater Forum*, 15, 85–96.
- Havas, M. & Rosseland, B.O. (1995) Response of zooplankton, benthos, and fish to acidification: an overview. *Water Air & Soil Pollution*, 85, 51–62. <https://doi.org/10.1007/BF00483688>
- Hayes, F.R. (1949) The growth, general chemistry, and temperature relations of salmonid eggs. *Quarterly Review of Biology*, 24, 281–308. <https://doi.org/10.1086/397213>
- Hayes, F.R., Wilmut, I.B. & Livingstone, D.A. (1951) The oxygen consumption of the salmon egg in relation to development and activity. *Journal of Experimental Zoology*, 116, 377–395. <https://doi.org/10.1002/jez.1401160302>
- Heggberget, T.G., Haukebo, T., Mork, J. & Ståhl, G. (1988) Temporal and spatial segregation of spawning in sympatric populations of Atlantic salmon, *Salmo salar* L., and brown trout, *Salmo trutta* L. *Journal of Fish Biology*, 33, 347–356. <https://doi.org/10.1111/j.1095-8649.1988.tb05477.x>
- HELCOM. (2011) *Salmon and Sea Trout Populations and Rivers in the Baltic Sea—HELCOM assessment of salmon (*Salmo salar*) and sea trout (*Salmo trutta*) populations and habitats in rivers flowing to the Baltic Sea*. Helsinki: Helsinki Commission, Baltic Marine Environment Protection Commission, pp. 82. Available at: <https://www.cbd.int/doc/meetings/mar/soiom-2016-01/other/soiom-2016-01-helcom-09-en.pdf>. [Accessed 6th Dec 2020].
- Hendry, K., Cragg-Hine, D., O'Grady, M., Sambrook, H. & Stephen, A. (2003) Management of habitat for rehabilitation and enhancement of salmonid stocks. *Fisheries Research*, 62, 171–192.
- Henriksen, A., Skogheim, O.K. & Rosseland, B.O. (1984) Episodic changes in pH and aluminium-speciation kill fish in a Norwegian salmon river. *Vatten*, 40, 255–260.
- Hering, D., Borja, A., Carstensen, J., Carvalho, L., Elliott, M., Feld, C.K. et al. (2010) The European Water Framework Directive at the age of 10: a critical review of the achievements with recommendations for the future. *Science of the Total Environment*, 408, 4007–4019. <https://doi.org/10.1016/j.scitotenv.2010.05.031>
- Hesthagen, T., Larsen, B.M., Bolstad, G., Fiske, P. & Jonsson, B. (2017) Mitigation of acidified salmon rivers—effects of liming on young brown trout *Salmo trutta*. *Journal of Fish Biology*, 91, 1350–1364. <https://doi.org/10.1111/jfb.13454>
- Heywood, M.J.T. & Walling, D.E. (2007) The sedimentation of salmonid spawning gravels in the Hampshire Avon catchment, UK: implications for the dissolved oxygen content of intragravel water and embryo survival. *Hydrological Processes*, 21, 770–788. <https://doi.org/10.1002/hyp.6266>
- Hinch, S.G. & Bratty, J. (2000) Effects of swim speed and activity pattern on success of adult sockeye salmon migration through an area of difficult passage. *Transactions of the American Fisheries Society*, 129, 598–606.
- Hoffmann, R.C. (1996) Economic development and aquatic ecosystems in medieval Europe. *American Historical Review*, 101, 631–669. <https://doi.org/10.1007/s10152-004-0203-5>
- Honkanen, J.O., Heinonen, J. & Kukkonen, J.V. (2001). Toxicokinetics of waterborne bisphenol A in landlocked salmon (*Salmo salar* m. Sebago) eggs at various temperatures. *Environmental Toxicology and Chemistry*, 20, 2296–2302. <https://doi.org/10.1002/etc.5620201023>
- Howells, G., Dalziel, T.R.K. & Turnpenny, A.W.H. (1992) Loch Fleet: liming to restore a brown trout fishery. *Environmental Pollution*, 78, 131–139.
- Hultberg, H. & Andersson, I.B. (1982) Liming of acidified lakes: induced long-term changes. *Water Air & Soil Pollution*, 18, 311–331. <https://doi.org/10.1007/BF02419420>
- Hunter, J.W. (1973) *A discussion of game fish in the State of Washington as related to water requirements*. Olympia WA: Washington State Dept. Game.
- Hutchings, J.A., Ardren, W.R., Barlaup, B.T., Bergman, E., Clarke, K.D., Greenberg, L.A. et al. (2019) Life-history variability and conservation status of landlocked Atlantic salmon: an overview. *Canadian Journal of Fisheries and Aquatic Sciences*, 76, 1697–1708. <https://doi.org/10.1139/cjfas-2018-0413>
- Hutchings, J.A. & Jones, M.E.B. (1998) Life history variation and growth rate thresholds for maturity in Atlantic salmon, *Salmo salar*. *Canadian Journal of Fisheries and Aquatic Science*, 55, 22–47.
- ICES. (2013). *Report of the Workshop on Sea Trout (WKTRUTTA)*, 12–14 November 2013. Copenhagen: ICES, pp. 243. ICES CM 2013/SSGEF:15.
- ICES. (2017b) *Report of the Workshop on Potential Impacts of Climate Change on Atlantic Salmon Stock Dynamics (WKCCISA)*. (ACOM:39). Copenhagen: ICES Advisory Committee. Available <http://www.ices.dk/sites/pub/Publication%20Reports/Expert%20Group%20>





- Report/acom/2017/WKCCISAL/wkccisal\_2017.pdf. [Accessed 10<sup>th</sup> Aug 2020].
- ICES. (2019a). *North Atlantic Salmon Stocks*. In Report of the ICES Advisory Committee, 2019. ICES Advice 2019, sal.oth.nasco. <https://doi.org/10.17895/ICES.advice.5230>
- ICES. (2019b). *Salmon (Salmo salar) in subdivisions 22–31 (Baltic Sea, excluding the Gulf of Finland)*. In Report of the ICES. Advisory Committee, 2019. ICES Advice 2019, sal.27.22–31. <https://doi.org/10.17895/ices.advice.4742>
- ICES. (2019c) *Working Group on North Atlantic Salmon (WGNAS)*. ICES Scientific Reports, 1, 1–368. <https://doi.org/10.17895/ices.pub.4978>
- ICES. (2017a). *Report of the Working Group on Effectiveness of Recovery Actions for Atlantic Salmon (WGERAAS)*, 9–13 November 2015. Copenhagen: ICES, pp. 115. ICES CM 2015/SSGEPD:03.
- ICPR. (2015). *Monitoring Rhine fish fauna 2012/2013 (228)*. Koblenz: International Commission for the Protection of the Rhine (IKSR, CIPR, ICBR). Available at: [https://www.iksr.org/fileadmin/user\\_upload/DKDM/Dokumente/Fachberichte/DE/rp\\_De\\_0228.pdf](https://www.iksr.org/fileadmin/user_upload/DKDM/Dokumente/Fachberichte/DE/rp_De_0228.pdf). [Accessed 11th July 2020].
- Ikediashi, C., Billington, S. & Stevens, J.R. (2012) The origins of Atlantic salmon (*Salmo salar* L.) recolonizing the River Mersey in north-west England. *Ecology and Evolution*, 2, 2532–2543. <https://doi.org/10.1002/ece3.353>
- Ikediashi, C., Paris, J.R., King, R.A., Beaumont, W.R.C., Ibbotson, A. & Stevens, J.R. (2018) Atlantic salmon *Salmo salar* in the chalk streams of England are genetically unique. *Journal of Fish Biology*, 92, 621–641.
- Ingendahl, D. (1999) *Der Reproduktionserfolg von Meerforelle und Lachs in Korrelation zu den Milieubedingungen des hyporheischen Interstitials*. Doctoral thesis. Cologne: University Cologne Hundt Druck GmbH.
- Ingendahl, D. (2001) Dissolved oxygen concentration and emergence of sea trout fry from natural redds in tributaries of the River Rhine. *Journal of Fish Biology*, 58, 325–341. <https://doi.org/10.1111/j.1095-8649.2001.tb02256.x>
- IPCC. (2007) *Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Geneva: IPCC, pp. 112. [https://www.ipcc.ch/site/assets/uploads/2018/02/ar4\\_syr\\_full\\_report.pdf](https://www.ipcc.ch/site/assets/uploads/2018/02/ar4_syr_full_report.pdf). [Accessed 6th July 2020].
- IPCC. (2014) *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge: Cambridge University Press, pp. 696. Available at: [https://www.ipcc.ch/site/assets/uploads/2018/02/WGIIAR5-PartB\\_FINAL.pdf](https://www.ipcc.ch/site/assets/uploads/2018/02/WGIIAR5-PartB_FINAL.pdf). [Accessed 6th July 2020].
- IWB & IDUS (Institut für Wasser und Boden Dr. Uhlmann & IDUS Biologische Analytisches Umweltlabor). (2012). *Untersuchungen zu Ammonium in ostsächsischen Bergbaufolgeseen*. Prepared for Sächsisches Landesamt für Umwelt, Landwirtschaft und Geologie, pp. 234. Available at: [https://www.umwelt.sachsen.de/umwelt/download/Abschlussbericht\\_TP\\_05\\_online.pdf](https://www.umwelt.sachsen.de/umwelt/download/Abschlussbericht_TP_05_online.pdf). [Accessed 9th Aug 2020].
- Jackson, A.L. (2011) Renewable energy vs. biodiversity: policy conflicts and the future of nature conservation. *Global Environmental Change*, 21, 1195–1208. <https://doi.org/10.1016/j.gloenvcha.2011.07.001>
- Jackson, M.C., Loewen, C.J., Vinebrooke, R.D. & Chimimba, C.T. (2015) Net effects of multiple stressors in freshwater ecosystems: a meta-analysis. *Global change biology*, 22, 180–189. <https://doi.org/10.1111/gcb.13028>
- Jensen, A.J., Johnsen, B.O. & Saksgård, L. (1989) Temperature requirements in Atlantic salmon (*Salmo salar*), brown trout (*Salmo trutta*), and Arctic char (*Salvelinus alpinus*) from hatching to initial feeding compared with geographic distribution. *Canadian Journal of Fisheries and Aquatic Sciences*, 46, 786–789. <https://doi.org/10.1139/f89-097>
- Jensen, K.W. & Snekvik, E. (1972) Low pH levels wipe out salmon and trout populations in southernmost Norway. *Ambio*, 1, 223–225.
- Jepsen, N., Aarestrup, K., Økland, F. & Rasmussen, G. (1998) Survival of radiotagged Atlantic salmon (*Salmo salar* L.)—and trout (*Salmo trutta* L.) smolts passing a reservoir during seaward migration. *Hydrobiologia*, 371, 347. <https://doi.org/10.1023/A:1017047527478>
- Jobling, M. (1997) Temperature and growth: modulation of growth rate via temperature change. In: Wood, C.M. & McDonald, D.G. (Eds.) *Global warming: implications for freshwater and marine fish*. Cambridge: Press Cambridge, pp. 225–254.
- Johansson, D., Ruohonen, K., Kiessling, A., Oppedal, F., Stiansen, J.E., Kelly, M. et al. (2006) Effect of environmental factors on swimming depth preferences of Atlantic salmon (*Salmo salar* L.) and temporal and spatial variations in oxygen levels in sea cages at a fjord site. *Aquaculture*, 254, 594–605. <https://doi.org/10.1016/j.aquaculture.2005.10.029>
- Johnsen, B.O., Arnekleiv, J.V., Asplin, L., Barlaup, B.T., Næsje, T.F., Rosseland, B.O. et al. (2011) Hydropower development—Ecological effects. In: Aas, Ø., Einum, S., Klemetsen, A. & Skurdal, J. (Eds.) *Atlantic salmon ecology*. Chichester: John Wiley & Sons Ltd, pp. 351–386.
- Johnsen, B.O. & Jenser, A.J. (1991) The gyrodactylus story in Norway. *Aquaculture*, 98, 289–302.
- Jonsson, B. & Jonsson, N. (2009) A review of the likely effects of climate change on anadromous Atlantic salmon *Salmo salar* and brown trout *Salmo trutta*, with particular reference to water temperature and flow. *Journal of Fish Biology*, 75, 2381–2447. <https://doi.org/10.1111/j.1095-8649.2009.02380.x>
- Jonsson, B. & Jonsson, N. (2011) *Ecology of Atlantic salmon and brown trout: habitat as a template for life history*. Dordrecht: Springer. <https://doi.org/10.1007/978-94-007-1189-1>
- Jonsson, B., Jonsson, N., Brodtkorb, E. & Ingebrigtsen, P.J. (2001) Life-history traits of brown trout vary with the size of small streams. *Functional Ecology*, 15, 310–317.
- Jonsson, B., Jonsson, N. & Jonsson, M. (2018) Water level influences migratory patterns of anadromous brown trout in small streams. *Ecology of Freshwater Fish*, 27, 1066–1075. <https://doi.org/10.1111/eff.12415>
- Jonsson, N. (1991) Influence of water flow, water temperature and light on fish migration in rivers. *Nordic Journal of Freshwater Research*, 66, 20–35.
- Jonsson, N., Jonsson, B. & Hansen, L.P. (1998) The relative role of density-dependent and density-independent survival in the life cycle of Atlantic salmon *Salmo salar*. *Journal of Animal Ecology*, 67, 751–762. <https://doi.org/10.1046/j.1365-2656.1998.00237.x>
- Jungwirth, M., Haidvogel, G., Moog, O., Muhar, S. & Schmutz, S. (2003) *Angewandte Fischökologie an Fließgewässern*. Wien: Facultas Universitätsverlag.
- Jungwirth, M. & Winkler, H. (1984) The temperature dependence of embryonic development of grayling (*Thymallus thymallus*), Danube salmon (*Hucho hucho*), Arctic char (*Salvelinus alpinus*) and brown trout (*Salmo trutta fario*). *Aquaculture*, 38, 315–327.
- Karlsson, S., Diserud, O.H., Fiske, P. & Hindar, K. (2016) Widespread genetic introgression of escaped farmed Atlantic salmon in wild salmon populations. *ICES Journal of Marine Science*, 73, 2488–2498. <https://doi.org/10.1093/icesjms/fsw121>
- Kazakov, R.V. (1992) Distribution of Atlantic salmon, *Salmo salar* L., in freshwater bodies of Europe. *Aquaculture Research*, 23, 461–475. <https://doi.org/10.1111/j.1365-2109.1992.tb00790.x>
- Kemp, P.S. (2012) Bridging the gap between fish behaviour, performance and hydrodynamics: an ecohydraulics approach to fish passage research. *River Research and Applications*, 28, 403–406. <https://doi.org/10.1002/rra.1599>
- Kemp, P.S. & O'hanley, J.R. (2010) Procedures for evaluating and prioritising the removal of fish passage barriers: a

- synthesis. *Fisheries Management and Ecology*, 17, 297–322. <https://doi.org/10.1111/j.1365-2400.2010.00751.x>
- Kemp, P., Sear, D., Collins, A., Naden, P. & Jones, I. (2011) The impacts of fine sediment on riverine fish. *Hydrological processes*, 25, 1800–1821. <https://doi.org/10.1002/hyp.7940>
- King, H.R., Pankhurst, N.W. & Watts, M. (2007) Reproductive sensitivity to elevated water temperatures in female Atlantic salmon is heightened at certain stages of vitellogenesis. *Journal of Fish Biology*, 70, 190–205. <https://doi.org/10.1111/j.1095-8649.2006.01295.x>
- King, H.R., Pankhurst, N.W., Watts, M. & Pankhurst, P.M. (2003) Effect of elevated summer temperatures on gonadal steroid production, vitellogenesis and egg quality in female Atlantic salmon. *Journal of Fish Biology*, 63, 153–167. <https://doi.org/10.1046/j.1095-8649.2003.00137.x>
- Kinouchi, T., Yagi, H. & Miyamoto, M. (2007) Increase in stream temperature related to anthropogenic heat input from urban wastewater. *Journal of Hydrology*, 335, 78–88. <https://doi.org/10.1016/j.jhydrol.2006.11.002>
- Klemetsen, A., Amundsen, P.A., Dempson, J.B., Jonsson, B., Jonsson, N., O'Connell, M.F. et al. (2003) Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecology of Freshwater Fish*, 12, 1–59. <https://doi.org/10.1034/j.1600-0633.2003.00010.x>
- Klütsch, C.F.C., Maduna, S.N., Polikarpova, N., Forfang, K., Aspholm, P.E., Nyman, T. et al. (2019) Genetic changes caused by restocking and hydroelectric dams in demographically bottlenecked brown trout in a transnational subarctic riverine system. *Ecology and Evolution*, 9, 6068–6081. <https://doi.org/10.1002/ece3.5191>
- Knott, J., Mueller, M., Pander, J. & Geist, J. (2019) Fish passage and injury risk at a surface bypass of a small-scale hydropower plant. *Sustainability*, 11, 6037. <https://doi.org/10.3390/su11216037>
- Kondolf, G.M. (2000) Assessing salmonid spawning gravel quality. *Transactions of the American Fisheries Society*, 129, 262–281.
- Kondolf, G.M., Williams, J.G., Horner, T.C. & Milan, D. (2008) Assessing physical quality of spawning habitat. *American Fisheries Society Symposium*, 65, 26.
- Kondolf, G.M. & Wolman, M.G. (1993) The sizes of salmonid spawning gravels. *Water Resource Research*, 29, 2275–2285. <https://doi.org/10.1029/93WR00402>
- Kottelat, M. & Freyhof, J. (2007) *Handbook of European freshwater fishes*. Berlin: Kottelat, Cornol and Freyhof.
- Kouwenberg, J.H.M., Browman, H.I., Cullen, J.J., Davis, R.F., St-Pierre, J.F. & Runge, J.A. (1999) Biological weighting of ultraviolet (280–400 nm) induced mortality in marine zooplankton and fish. I. Atlantic cod (*Gadus morhua*) eggs. *Marine Biology*, 134, 269–284. <https://doi.org/10.1007/s002270050545>
- Kristensen, P., Whalley, C., Zal, F.N.N. & Christiansen, T. (2018). *European waters assessment of status and pressures 2018*. EEA Report, (7/2018).
- Kuhn, J., Casas-Mulet, R., Pander, J. & Geist, J. (2021) Assessing stream thermal heterogeneity and cold-water patches from UAV-based imagery: a matter of classification methods and metrics. *Remote Sensing*, 13, 1379. <https://doi.org/10.3390/rs13071379>
- Lacroix, G.L. (1985a) Survival of eggs and alevins of Atlantic salmon (*Salmo salar*) in relation to the chemistry of interstitial water in redds in some acidic streams of Atlantic Canada. *Canadian Journal of Fisheries and Aquatic Sciences*, 42, 292–299. <https://doi.org/10.1139/f85-037>
- Lacroix, G.L., Gordon, D.J. & Johnston, D.J. (1985b) Effects of low environmental pH on the survival, growth, and ionic composition of postemergent Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, 42, 768–775. <https://doi.org/10.1139/f85-098>
- Landergren, P. (2004) Factors affecting early migration of sea trout *Salmo trutta* parr to brackish water. *Fisheries Research*, 67, 283–294. <https://doi.org/10.1016/j.fishres.2003.10.005>
- Lauridsen, R.B., Moore, A., Gregory, S.D., Beaumont, W.R.C., Privitera, L. & Kavanagh, J.A. (2017) Migration behaviour and loss rate of trout smolts in the transitional zone between freshwater and saltwater. In: Harris, G. (Ed.) *Sea trout: Science & Management. Proceedings of the 2nd International Sea Trout Symposium*. Leicester: Metador by Troubador Publishing Ltd., pp. 292–307.
- Leivestad, H. & Muniz, I.P. (1976) Fish kills at low pH in a Norwegian river. *Nature*, 259, 391–392. <https://doi.org/10.1038/259391a0>
- Lenders, H.J.R., Chamuleau, T.P.M., Hendriks, A.J., Lauwerier, R.C.G.M., Leuven, R.S.E.W. & Verberk, W.C.E.P. (2016) Historical rise of waterpower initiated the collapse of salmon stocks. *Scientific Reports*, 6, 29269. <https://doi.org/10.1038/srep29269>
- Lenhart, B. & Steinberg, C. (1984) *Limnochemische und limnobiologische Auswirkungen der Versauerung von kalkarmen Oberflächengewässern - Eine Literaturstudie*. München: Informationsberichte Bayerisches Landesamtes für Wasserwirtschaft, p. 4.
- LfU. (2005) *Mindestabflüsse in Ausleitungsstrecken*. Fischereiforschungsstelle Baden-Württemberg, pp. 30. Available at: [http://www.marcosander.de/pdf/anforderungsprofile\\_indikatorfischarten.pdf](http://www.marcosander.de/pdf/anforderungsprofile_indikatorfischarten.pdf). [Accessed 22nd Oct 2020].
- Liao, P.B. & Mayo, R.D. (1972) Salmonid hatchery water reuse systems. *Aquaculture*, 1, 317–335. [https://doi.org/10.1016/0044-8486\(72\)90033-6](https://doi.org/10.1016/0044-8486(72)90033-6)
- Lobón-Cerviá, J. (2009) Why, when and how do fish populations decline, collapse and recover? The example of brown trout (*Salmo trutta*) in Rio Chaballos (northwestern Spain). *Freshwater Biology*, 54, 1149–1162. <https://doi.org/10.1111/j.1365-2427.2008.02159.x>
- Lobón-Cerviá, J. (2017) Introduction: princess of the streams: the brown trout *Salmo trutta* L. as aquatic royalty. In: Lobón-Cerviá, J. & Sanz, N. (Eds.) *Brown trout: biology, ecology and management*. Hoboken: John Wiley & Sons Ltd, pp. 1–13. <https://doi.org/10.1002/9781119268352.ch1>
- Lobón-Cerviá, J. & Rincón, P.A. (2004) Environmental determinants of recruitment and their influence on the population dynamics of stream-living brown trout *Salmo trutta*. *Oikos*, 105, 641–646. <https://doi.org/10.1111/j.0030-1299.2004.12989.x>
- 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. <https://doi.org/10.1002/rra.1072>
- Louhi, P., Ovaska, M., Mäki-Petäys, A., Erkinaro, J. & Muotka, T. (2011) Does fine sediment constrain salmonid alevin development and survival? *Canadian Journal of Fisheries and Aquatic Sciences*, 68, 1819–1826. <https://doi.org/10.1139/f2011-106>
- 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*, 73, 1733–1741. <https://doi.org/10.1139/cjfas-2015-0546>
- Lundqvist, H., Rivinoja, P., Leonardsson, K. & McKinnell, S. (2008) Upstream passage problems for wild Atlantic salmon (*Salmo salar* L.) in a regulated river and its effect on the population. In: Dufour, S., Prévost, E., Rochard, E. & Williot, P. (Eds.) *Fish and Diadromy in Europe (ecology, management, conservation)*. Dordrecht: Springer, pp. 111–127. [https://doi.org/10.1007/978-1-4020-8548-2\\_9](https://doi.org/10.1007/978-1-4020-8548-2_9)
- MacCrimmon, H.R. & Gots, B.L. (1979) World distribution of Atlantic salmon, *Salmo salar*. *Journal of the Fisheries Board of Canada*, 36, 422–457. <https://doi.org/10.1139/f79-062>
- Machordom, A., Garcia-Marin, J.L., Sanz, N., Almodovar, A. & Pla, C. (1999) Allozyme diversity in brown trout (*Salmo trutta*) from Central Spain: genetic consequences of restocking. *Freshwater Biology*, 41, 707–717. <https://doi.org/10.1046/j.1365-2427.1999.00418.x>
- Malaj, E., Peter, C., Grote, M., Kühne, R., Mondy, C.P., Usseglio-Polatera, P. et al. (2014) Organic chemicals jeopardize the health of freshwater ecosystems on the continental scale. *Proceedings of the National Academy of Sciences*, 111, 9549–9554. <https://doi.org/10.1073/pnas.1321082111>



- Malcolm, I.A., Soulsby, C., Youngson, A.F. & Petry, J. (2003a) Heterogeneity in ground water-surface water interactions in the hyporheic zone of a salmonid spawning stream. *Hydrological Processes*, 17, 601–617. <https://doi.org/10.1002/hyp.1156>
- Malcolm, I., Youngson, A.F., Greig, S. & Soulsby, C. (2008) Hyporheic influences on spawning success. In: Sear, D. & DeVries, P. (Eds.) *Salmon spawning habitat in rivers: physical controls, biological responses and approaches to remediation*. Bethesda: American Fisheries Society, pp. 225–248.
- Malcolm, I.A., Youngson, A.F. & Soulsby, C. (2003b) Survival of salmonid eggs in a degraded gravel-bed stream: effects of groundwater-surface water interactions. *River Research and Applications*, 19, 303–316. <https://doi.org/10.1002/rra.706>
- Marzano, F.N., Corradi, N., Papa, R., Tagliavini, J. & Gandolfi, G. (2003) Molecular evidence for introgression and loss of genetic variability in *Salmo (trutta) macrostigma* as a result of massive restocking of Apennine populations (Northern and Central Italy). *Environmental Biology of Fishes*, 68, 349–356. <https://doi.org/10.1023/B:EBFI.0000005762.81631.f>
- Matthews, M.A., Poole, W.R., Thompson, C.E., McKillen, J., Ferguson, A., Hindar, K. et al. (2000) Incidence of hybridization between Atlantic salmon, *Salmo salar* L., and brown trout, *Salmo trutta* L., in Ireland. *Fisheries Management and Ecology*, 7, 337–347. <https://doi.org/10.1046/j.1365-2400.2000.00208.x>
- McCormick, S.D., Hansen, L.P., Quinn, T.P. & Saunders, R.L. (1998) Movement, migration, and smolting of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, 55, 77–92. <https://doi.org/10.1139/d98-011>
- McGinnity, P., Prodöhl, P., Ferguson, A., Hynes, R., Maoiléidigh, N.O., Baker, N. et al. (2003) Fitness reduction and potential extinction of wild populations of Atlantic salmon, *Salmo salar*, as a result of interactions with escaped farm salmon. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 270, 2443–2450. <https://doi.org/10.1098/rspb.2003.2520>
- McGinnity, P., Stone, C., Taggart, J.B., Cooke, D., Cotter, D., Hynes, R. et al. (1997) Genetic impact of escaped farmed Atlantic salmon (*Salmo salar* L.) on native populations: use of DNA profiling to assess freshwater performance of wild, farmed, and hybrid progeny in a natural river environment. *ICES Journal of Marine Science*, 54, 998–1008. [https://doi.org/10.1016/S1054-3139\(97\)80004-5](https://doi.org/10.1016/S1054-3139(97)80004-5)
- McLaughlin, R.L., Smyth, E.R., Castro-Santos, T., Jones, M.L., Koops, M.A., Pratt, T.C. et al. (2013) Unintended consequences and trade-offs of fish passage. *Fish and Fisheries*, 14, 580–604. <https://doi.org/10.1111/faf.12003>
- Mills, D. (1971). *Salmon and trout*. Edinburgh: Oliver & Boyd.
- Mills, D. (1989) *Ecology and management of Atlantic salmon*. London: Chapman & Hall.
- Mitchell, S.C. & Cunjak, R.A. (2007) Stream flow, salmon and beaver dams: roles in the construction of stream fish communities within an anadromous salmon dominated stream. *Journal of Animal Ecology*, 76, 1062–1074. <https://doi.org/10.1111/j.1365-2656.2007.01286.x>
- Mohammed, A. (2013) Why are early life stages of aquatic organisms more sensitive to toxicants than adults? *New insights into toxicity and drug testing*, 3, 49–62. <https://doi.org/10.5772/55187>
- Monnerjahn, U. (2011) Atlantic salmon (*Salmo salar* L.) re-introduction in Germany: a status report on national programmes and activities. *Journal of Applied Ichthyology*, 27, 33–40. <https://doi.org/10.1111/j.1439-0426.2011.01849.x>
- Moreau, D.A. & Moring, J.R. (1993) *Refinement and testing of the habitat suitability index model for Atlantic salmon*. Technical report prepared for US Fish and Wildlife Service. Orono: Maine Cooperative Research Unit.
- Mueller, M., Bierschenk, A.M., Bierschenk, B.M., Pander, J. & Geist, J. (2020) Effects of multiple stressors on the distribution of fish communities in 203 headwater streams of Rhine, Elbe and Danube. *Science of the Total Environment*, 703, 134523. <https://doi.org/10.1016/j.scitotenv.2019.134523>
- Mueller, M., Pander, J. & Geist, J. (2014) The ecological value of stream restoration measures: an evaluation on ecosystem and target species scales. *Ecological Engineering*, 62, 129–139. <https://doi.org/10.1016/j.ecoleng.2013.10.030>
- Mueller, M., Pander, J. & Geist, J. (2017) Evaluation of external fish injury caused by hydropower plants based on a novel field-based protocol. *Fisheries Management and Ecology*, 24, 240–255. <https://doi.org/10.1111/fme.12229>
- Nagel, C., Pander, J., Mueller, M. & Geist, J. (2020) Substrate composition determines emergence success and development of European nase larvae (*Chondrostoma nasus* L.). *Ecology of Freshwater Fish*, 29, 121–131. <https://doi.org/10.1111/eff.12500>
- NASCO. (2018). *North Atlantic Salmon stocks*. In: Report of the ICES Advisory Committee. ICES Advice 2019, sal.oth.nasco. <https://doi.org/10.17895/ices.pub.4335>
- NASCO. (2019) *State of North Atlantic Salmon*. Available at: <http://www.nasco.int/pdf/iys/SoS-final-online.pdf>. [Accessed 7th June 2020].
- Nielsen, E.E., Hansen, M.M. & Bach, L.A. (2001) Looking for a needle in a haystack: discovery of indigenous Atlantic salmon (*Salmo salar* L.) in stocked populations. *Conservation Genetics*, 2, 219–232.
- Niepagenkemper, O., Schulte, U., Meyer, E., Bode, H., Nusch, E. & Weyand, M. (2003) *Pilotmassnahmen zur Verbesserung der Beschaffenheit von Geschiebebaenken in Laichgewaessern von Salmoniden im Ruhrsystem*. Muenster: Ruhrverband Muenster.
- Nilsson, C., Reidy, C.A., Dynesius, M. & Revenga, C. (2005) Fragmentation and flow regulation of the world's river systems. *Science*, 308, 405–408. <https://doi.org/10.1126/science.1107887>
- Noonan, M.J., Grant, J.W. & Jackson, C.D. (2012) A quantitative assessment of fish passage efficiency. *Fish and Fisheries*, 13, 450–464. <https://doi.org/10.1111/j.1467-2979.2011.00445.x>
- Northcote, T.G. (1995) Comparative biology and management of Arctic and European grayling (Salmonidae, *Thymallus*). *Reviews in Fish Biology and Fisheries*, 5, 141–194. <https://doi.org/10.1007/BF00179755>
- O'Hanley, J.R. (2011) Open rivers: barrier removal planning and the restoration of free-flowing rivers. *Journal of Environmental Management*, 92, 3112–3120. <https://doi.org/10.1016/j.jenvman.2011.07.027>
- Ockenden, M.C., Deasy, C., Quinton, J.N., Bailey, A.P., Surridge, B. & Stoate, C. (2012) Evaluation of field wetlands for mitigation of diffuse pollution from agriculture: Sediment retention, cost and effectiveness. *Environmental Science & Policy*, 24, 110–119. <https://doi.org/10.1016/j.envsci.2012.06.003>
- Ojanguren, A.F. & Braña, F. (2003) Thermal dependence of embryonic growth and development in brown trout. *Journal of Fish Biology*, 62, 580–590. <https://doi.org/10.1046/j.0022-1112.2003.00049.x>
- Ojanguren, A.F., Reyes-Gavilán, F.G. & Muñoz, R.R. (1999) Effects of temperature on growth and efficiency of yolk utilisation in eggs and pre-feeding larval stages of Atlantic salmon. *Aquaculture International*, 7, 81–87. <https://doi.org/10.1023/A:1009214804949>
- Olsson, I.C., Greenberg, L.A., Bergman, E. & Wysujack, K. (2006) Environmentally induced migration: the importance of food. *Ecology Letters*, 9, 645–651. <https://doi.org/10.1111/j.1461-0248.2006.00909.x>
- Oppen-Berntsen, D.O., Bogsnes, A. & Walther, B.T. (1990) The effects of hypoxia, alkalinity and neurochemicals on hatching of Atlantic salmon (*Salmo salar*) eggs. *Aquaculture*, 86, 417–430. [https://doi.org/10.1016/0044-8486\(90\)90330-P](https://doi.org/10.1016/0044-8486(90)90330-P)
- Opperman, J.J., Moyle, P.B., Larsen, E.W., Florsheim, J.L. & Manfree, A.D. (2017) *Floodplains: Processes and management for ecosystem services*. Oakland: University of California Press.
- Ormerod, S.J., Dobson, M., Hildrew, A.G. & Townsend, C. (2010) Multiple stressors in freshwater ecosystems. *Freshwater Biology*, 55, 1–4. <https://doi.org/10.1111/j.1365-2427.2009.02395.x>

- ORSANCO. (1955) Aquatic life water quality criteria. *Sewage ind. Wastes*, 27, 321–331.
- Ottaway, E.M., Carling, P.A., Clarke, A. & Reader, N.A. (1981) Observations on the structure of brown trout, *Salmo trutta* Linnaeus, redds. *Journal of Fish Biology*, 19, 593–607. <https://doi.org/10.1111/j.1095-8649.1981.tb03825.x>
- Overrein, L., Seip, H.M. & Tollan, A. (1980). *Acid precipitation-Effects on forest and fish*. Oslo-As: Final report of the SNSF-project 1972-1980, pp. 175.
- Ozerov, M.Y., Veselov, A.E., Lumme, J. & Primmer, C.R. (2012) "Riverscape" genetics: river characteristics influence the genetic structure and diversity of anadromous and freshwater Atlantic salmon (*Salmo salar*) populations in northwest Russia. *Canadian Journal of Fisheries and Aquatic Sciences*, 69, 1947–1958. <https://doi.org/10.1139/f2012-114>
- Pander, J. & Geist, J. (2010) Salmonid-egg floating boxes as bio-indication for riverine water quality and stocking success. *Journal of Fish Biology*, 76, 2584–2590. <https://doi.org/10.1111/j.1095-8649.2010.02645.x>
- Pander, J. & Geist, J. (2013) Ecological indicators for stream restoration success. *Ecological Indicators*, 30, 106–118. <https://doi.org/10.1016/j.ecolind.2013.01.039>
- Pander, J. & Geist, J. (2016) Can fish habitat restoration for rheophilic species in highly modified rivers be sustainable in the long run? *Ecological Engineering*, 88, 28–38. <https://doi.org/10.1016/j.ecoleng.2015.12.006>
- 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. <https://doi.org/10.1002/rra.2732>
- Pander, J., Mueller, M. & Geist, J. (2018) Habitat diversity and connectivity govern the conservation value of restored aquatic floodplain habitats. *Biological Conservation*, 217, 1–10. <https://doi.org/10.1016/j.biocon.2017.10.024>
- 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. <https://doi.org/10.1111/j.1095-8649.2008.02145.x>
- Pankhurst, N.W., King, H.R., Anderson, K., Elizur, A., Pankhurst, P.M. & Ruff, N. (2011) Thermal impairment of reproduction is differentially expressed in maiden and repeat spawning Atlantic salmon. *Aquaculture*, 316, 77–87. <https://doi.org/10.1016/j.aquaculture.2011.03.009>
- Parker, H. & Rønning, Ø.C. (2007) Low potential for restraint of anadromous salmonid reproduction by beaver *Castor fiber* in the Numedalslågen river catchment, Norway. *River Research and Applications*, 23, 752–762. <https://doi.org/10.1002/rra.1008>
- Parkhurst, B.R., Bergman, H.L., Fernandez, J., Gulley, D.D., Hockett, J.R. & Sanchez, D.A. (1990) Inorganic monomeric aluminium and pH as predictors of acidic water toxicity to brook trout (*Salvelinus fontinalis*). *Canadian Journal of Fisheries and Aquatic Sciences*, 47, 1631–1640. <https://doi.org/10.1139/f90-185>
- Parrish, D.L., Behnke, R.J., Gephard, S.R., McCormick, S.D. & Reeves, G.H. (1998) Why aren't there more Atlantic salmon (*Salmo salar*)? *Canadian Journal of Fisheries and Aquatic Sciences*, 55, 281–287.
- Parry, E.S.D., Lauridsen, R.B. & Griffiths, S. (2018) The effects of flow on Atlantic salmon (*Salmo salar*) redd distribution in a UK chalk stream between 1980 and 2015. *Ecology of Freshwater Fish*, 27, 128–137. <https://doi.org/10.1111/eff.12330>
- Peake, S., McKinley, R.S. & Scruton, D.A. (1997) Swimming performance of various freshwater Newfoundland salmonids relative to habitat selection and fishway design. *Journal of Fish Biology*, 51, 710–723. <https://doi.org/10.1111/j.1095-8649.1997.tb01993.x>
- Peter, A. (1998) Interruption of the river continuum by barriers and the consequences for migratory fish. In: Jungwirth, M., Schmutz, S. & Weiss, S. (Eds.) *Fish migration and fish bypasses*. Oxford: Fishing News Books.
- Peterson, R.H., Daye, P.G. & Metcalfe, J.L. (1980) Inhibition of Atlantic salmon (*Salmo salar*) hatching at low pH. *Canadian Journal of Fisheries and Aquatic Sciences*, 37, 770–774. <https://doi.org/10.1139/f80-103>
- Pflugrath, B.D., Boys, C.A., Cathers, B. & Deng, Z.D. (2019) Over or under? Autonomous sensor fish reveals why overshot weirs may be safer than undershot weirs for fish passage. *Ecological Engineering*, 132, 41–48. <https://doi.org/10.1016/j.ecoleng.2019.03.010>
- Piper, R.G., McElwain, I.B., Orme, L.E., McCraren, J.P., Fowler, L.G. & Leonard, J.R. (1982) *Fish hatchery management*. Washington: U.S. Fish Wildlife Service.
- Poe, T.P., Hansel, H.C., Vigg, S., Palmer, D.E. & Prendergast, L.A. (1991) Feeding of predaceous fishes on out-migrating juvenile salmonids in John Day Reservoir, Columbia River. *Transactions of the American Fisheries Society*, 120, 405–420.
- Poff, N.L., Allan, J.D., Bain, M.B., Karr, J.R., Prestegard, K.L., Richter, B.D. et al. (1997) The natural flow regime. *BioScience*, 47, 769–784. <https://doi.org/10.2307/1313099>
- Poff, N.L., Allan, J.D., Palmer, M.A., Hart, D.D., Richter, B.D., Arthington, A.H. et al. (2003) River flows and water wars: emerging science for environmental decision making. *Frontiers in Ecology and the Environment*, 1, 298–306.
- Pokki, H., Artell, J., Mikkola, J., Orell, P. & Ovaskainen, V. (2018) Valuing recreational salmon fishing at a remote site in Finland: a travel cost analysis. *Fisheries Research*, 208, 145–156. <https://doi.org/10.1016/j.fishres.2018.07.013>
- Porter, T.R., Healey, M.C., O'Connell, M.F., Baum, E.T., Bielak, A.T. & Côté, Y. (1986) Implications of varying the sea age at maturity of Atlantic salmon (*Salmo salar*) on yield to the fisheries. *Canadian Special Publication in Fisheries and Aquatic Sciences*, 89, 110–117.
- Power, G. (1958) The evolution of the freshwater races of the Atlantic salmon (*Salmo salar* L.) in eastern North America. *Arctic*, 11, 86–92.
- Poxton, M.G. (1991) Incubation of salmon eggs and rearing of alevins: natural temperature fluctuations and their influence on hatchery requirements. *Aquacultural Engineering*, 10, 31–53. [https://doi.org/10.1016/0144-8609\(91\)90009-9](https://doi.org/10.1016/0144-8609(91)90009-9)
- Pulg, U. (2009) *Laichplätze der Bachforelle (Salmo trutta) in der Moosach - Bewertung ihrer Funktionsfähigkeit, ihre Degradierung und ihre Restaurierung*. Doctoral thesis. Freising: Technical University Munich.
- Pulg, U., Barlaup, B.T., Sternecker, K., Trepl, L. & Unfer, G. (2013) Restoration of spawning habitats of brown trout (*Salmo trutta*) in a regulated chalk stream. *River Research and Applications*, 29, 172–182. <https://doi.org/10.1002/rra.1594>
- Quinn, T.P. (2005) *The behavior and ecology of Pacific salmon and trout*. Seattle: University of Washington Press.
- Quinn, T.P. & Buck, G.B. (2001) Size- and sex-selective mortality of adult sockeye salmon: bears, gulls, and fish out of water. *Transactions of the American Fisheries Society*, 130, 995–1005.
- Raleigh, R.F., Zuckerman, L.D. & Nelson, P.C. (1984) *Habitat suitability index models and instream flow suitability curves: brown trout*. Washington, DC: U.S. Fish and Wildlife Service Biological Report 82.
- Raleigh, R.F., Zuckerman, L.D. & Nelson, P.C. (1986) *Habitat suitability index models and instream flow suitability curves: brown trout*. Washington, DC: U.S. Fish and Wildlife Service Biological Report 82.
- Randak, T., Kocour, M., Žlábek, V., Polícar, T. & Jarkovský, J. (2006) Effect of culture conditions on reproductive traits of brown trout *Salmo trutta* L. *Bulletin Français De La Pêche Et De La Pisciculture.*, 383, 1–12. <https://doi.org/10.1051/kmae:2006001>
- Reader, J.P., Dalziel, T.R.K., Morris, R., Sayer, M.D.J. & Dempsey, C.H. (1991) Episodic exposure to acid and aluminium in soft water: survival and recovery of brown trout, *Salmo trutta* L. *Journal of Fish Biology*, 39, 181–196. <https://doi.org/10.1111/j.1095-8649.1991.tb04355.x>



- Reimchen, T.E. (2018) Diverse ecological pathways of salmon nutrients through an intact marine-terrestrial interface. *The Canadian Field-Naturalist*, 131, 350–368. <https://doi.org/10.22621/cfn.v131i4.1965>
- Rombough, P.J. (1988) Respiratory gas exchange, aerobic metabolism, and effects of hypoxia during early life. *Fish Physiology*, 11, 59–161. [https://doi.org/10.1016/S1546-5098\(08\)60199-5](https://doi.org/10.1016/S1546-5098(08)60199-5)
- Roni, P., Beechie, T., Pess, G. & Hanson, K. (2015) Wood placement in river restoration: fact, fiction, and future direction. *Canadian Journal of Fisheries and Aquatic Sciences*, 72, 466–478. <https://doi.org/10.1139/cjfas-2014-0344>
- Rosell, F., Bozser, O., Collen, P. & Parker, H. (2005) Ecological impact of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems. *Mammal review*, 35, 248–276. <https://doi.org/10.1111/j.1365-2907.2005.00067.x>
- Rosenberg, A. (2008) The price of lice. *Nature*, 451, 23–24. <https://doi.org/10.1038/451023a>
- Rozas-Serri, M. (2019) Gill diseases in marine salmon aquaculture with an emphasis on amoebic gill disease. *Atlantic*, 32, 34–35. <https://doi.org/10.1079/PAVSNR201914032>
- Rubin, J.F. (1998) Survival and emergence pattern of sea trout fry in substrata of different compositions. *Journal of Fish Biology*, 53, 84–92. <https://doi.org/10.1111/j.1095-8649.1998.tb00111.x>
- Rubin, J.-F. & Glimsater, C. (1996) Egg-to-fry survival of the sea trout in some streams of Gotland. *Journal of Fish Biology*, 48, 585–606. <https://doi.org/10.1111/j.1095-8649.1996.tb01454.x>
- Ruiz, A.F. & Rodríguez de los Santos, M. (2001) *Libro rojo de los vertebrados amenazados de Andalucía*. Sevilla: Consejería de Medio Ambiente Junta de Andalucía, pp. 321.
- Russell, I.C., Arahamian, M.W., Barry, J., Davidson, I.C., Fiske, P., Ibbotson, A.T. et al. (2012) The influence of the freshwater environment and the biological characteristics of Atlantic salmon smolts on their subsequent marine survival. *ICES Journal of Marine Science*, 69, 1563–1573.
- Rytwinski, T., Algera, D.A., Taylor, J.J., Smokorowski, K.E., Bennett, J.R., Harrision, P.M. et al. (2017) What are the consequences of fish entrainment and impingement associated with hydroelectric dams on fish productivity? A systematic review protocol. *Environmental Evidence*, 6, 8. <https://doi.org/10.1186/s13750-017-0087-x>
- Saltveit, S.J. & Brabrand, Å. (2013) Incubation, hatching and survival of eggs of Atlantic salmon (*Salmo salar*) in spawning redds influenced by groundwater. *Limnologica*, 43, 325–331. <https://doi.org/10.1016/j.limno.2013.05.009>
- Saltveit, S.J., 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. <https://doi.org/10.1002/rrr.652>
- Sayer, M.D.J., Reader, J.P. & Morris, R. (1991) Embryonic and larval development of brown trout, *Salmo trutta* L.: exposure to aluminium, copper, lead or zinc in soft, acid water. *Journal of Fish Biology*, 38, 431–455. <https://doi.org/10.1111/j.1095-8649.1991.tb03132.x>
- Schmutz, S., Bakken, T.H., Friedrich, T., Greimel, F., Harby, A., Jungwirth, M. et al. (2015) Response of fish communities to hydrological and morphological alterations in hydropeaking rivers of Austria. *River Research and Applications*, 31, 919–930. <https://doi.org/10.1002/rra.2795>
- Schofield, C.L. (1976) Acid precipitation: effects on fish. *Ambio*, 5, 228–230.
- Serbezov, D., Bernatchez, L., Olsen, E.M. & Vøllestad, L.A. (2010) Mating patterns and determinants of individual reproductive success in brown trout (*Salmo trutta*) revealed by parentage analysis of an entire stream living population. *Molecular Ecology*, 19, 3193–3205. <https://doi.org/10.1111/j.1365-294X.2010.04744.x>
- Sergeant, C.J., Bellmore, J.R., McConnell, C. & Moore, J.W. (2017) High salmon density and low discharge create periodic hypoxia in coastal rivers. *Ecosphere*, 8, e01846. <https://doi.org/10.1002/ecs2.1846>
- Serrano, I., Buffam, I., Palm, D., Brännäs, E. & Laudon, H. (2008) Thresholds for survival of brown trout during the spring flood acid pulse in streams high in dissolved organic carbon. *Transactions of the American Fisheries Society*, 137, 1363–1377. <https://doi.org/10.1577/T07-069.1>
- Silva, A.T., Lucas, M.C., Castro-Santos, T., Katopodis, C., Baumgartner, L.J., Thiem, J.D. et al. (2018) The future of fish passage science, engineering, and practice. *Fish and Fisheries*, 19, 340–362. <https://doi.org/10.1111/faf.12258>
- Skjelkvåle, B.L., Evans, C., Larssen, T., Hindar, A. & Raddum, G.G. (2003) Recovery from acidification in European surface waters: a view to the future. *Ambio*, 32, 170–175. <https://doi.org/10.1579/0044-7447-32.3.170>
- Skjelkvåle, B.L., Stoddard, J.L. & Andersen, T. (2001) Trends in surface waters acidification in Europe and North America (1989–1998). *Water, Air, & Soil Pollution*, 130, 787–792. <https://doi.org/10.1023/A:1013806223310>
- Skogheim, O.K. & Rosseland, B.O. (1984) A comparative study on salmonid fish species in acid aluminium-rich water, 1: Mortality of eggs and alevins. *Report - Institute of Freshwater Research*, 61, 177–185.
- Smialek, N., Pander, J., Mueller, M., Van Treeck, R., Wolter, C. & Geist, J. (2019) Do we know enough to save european riverine fish?—a systematic review on autecological requirements during critical life stages of 10 rheophilic species at risk. *Sustainability*, 11, 5011. <https://doi.org/10.3390/su11185011>
- Smith, G.W., Smith, I.P. & Armstrong, S.M. (1994) The relationship between river flow and entry to the Aberdeenshire Dee by returning adult Atlantic salmon. *Journal of Fish Biology*, 45, 953–960. <https://doi.org/10.1111/j.1095-8649.1994.tb01065.x>
- Solomon, D.J. & Sambrook, H.T. (2004) Effects of hot dry summers on the loss of Atlantic salmon, *Salmo salar*, from estuaries in South West England. *Fisheries Management and Ecology*, 11, 353–363. <https://doi.org/10.1111/j.1365-2400.2004.00403.x>
- Soulsby, C., Youngson, A.F., Moir, H.J. & Malcolm, I.A. (2001) Fine sediment influence on salmonid spawning habitat in a lowland agricultural stream: a preliminary assessment. *Science of the Total Environment*, 265, 295–307.
- Spromberg, J.A. & Meador, J.P. (2005) Relating results of chronic toxicity responses to population-level effects: Modeling effects on wild chinook salmon populations. *Integrated Environmental Assessment and Management: An International Journal*, 1, 9–21.
- Sternecker, K., Cowley, D.E. & Geist, J. (2013a) Factors influencing the success of salmonid egg development in river substratum. *Ecology of Freshwater Fish*, 22, 322–333. <https://doi.org/10.1111/eff.12020>
- Sternecker, K., Denic, M. & Geist, J. (2014) Timing matters: species-specific interactions between spawning time, substrate quality, and recruitment success in three salmonid species. *Ecology and Evolution*, 4, 2749–2758. <https://doi.org/10.1002/ece3.1128>
- Sternecker, K. & Geist, J. (2010) The effects of stream substratum composition on the emergence of salmonid fry. *Ecology of Freshwater Fish*, 19, 537–544. <https://doi.org/10.1111/j.1600-0633.2010.00432.x>
- 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. <https://doi.org/10.1007/s10641-013-0111-0>
- Stoddard, J.L., Jeffries, D.S., Liikewille, A., Clair, T.A., Dillon, P.J., Driscoll, C.T. et al. (1999) Regional trends in aquatic recovery from acidification in North America and Europe 1980–95. *Nature*, 401, 575–578. <https://doi.org/10.1038/44114>
- Stuart, T.A. (1962) The leaping behaviour of salmon and trout at falls and obstructions. *Freshwater and Salmon Fisheries Research*, 28, 1–46.

- Svendsen, J.C., Koed, A. & Aarestrup, K. (2004) Factors influencing the spawning migration of female anadromous brown trout. *Journal of Fish Biology*, *64*, 528–540. <https://doi.org/10.1111/j.0022-1112.2004.00319.x>
- Szałkiewicz, E., Jusik, S. & Grygoruk, M. (2018) Status of and perspectives on river restoration in Europe: 310,000 Euros per hectare of restored river. *Sustainability*, *10*, 129. <https://doi.org/10.3390/su10010129>
- Taubert, J.E. & Geist, J. (2017) The relationship between the freshwater pearl mussel (*Margaritifera margaritifera*) and its hosts. *Biology Bulletin*, *44*, 67–73. <https://doi.org/10.1134/S1062359017010149>
- Tetzlaff, D., Gibbins, C., Bacon, P.J., Youngson, A.F. & Soulsby, C. (2008) Influence of hydrological regimes on the pre-spawning entry of Atlantic salmon (*Salmo salar* L.) into an upland river. *River Research and Applications*, *24*, 528–542. <https://doi.org/10.1002/rra.1144>
- Thomaz, D.M.P.F., Beall, E. & Burke, T. (1997) Alternative reproductive tactics in Atlantic salmon: factors affecting mature parr success. *Proceedings of the Royal Society B: Biological Sciences*, *264*, 219–226. <https://doi.org/10.1098/rspb.1997.0031>
- Thompson, C.E., Poole, W.R., Matthews, M.A. & Ferguson, A. (1998) Comparison, using minisatellite DNA profiling, of secondary male contribution in the fertilisation of wild and ranched Atlantic salmon (*Salmo salar*) ova. *Canadian Journal of Fisheries and Aquatic Sciences*, *55*, 2011–2018. <https://doi.org/10.1139/cjfas-55-9-2011>
- Thorpe, J.E., Miles, M.S. & Keay, D.S. (1984) Developmental rate, fecundity and egg size in Atlantic salmon, *Salmo salar* L. *Aquaculture*, *43*, 289–305. [https://doi.org/10.1016/0044-8486\(84\)90030-9](https://doi.org/10.1016/0044-8486(84)90030-9)
- Thorstad, E.B., Heggberget, T.G. & Økland, F. (1998) Migratory behaviour of adult wild and escaped farmed Atlantic salmon, *Salmo salar* L., before, during and after spawning in a Norwegian river. *Aquaculture Research*, *29*, 419–428. <https://doi.org/10.1046/j.1365-2109.1998.00218.x>
- Thorstad, E.B., Todd, C.D., Uglem, I., Bjørn, P.A., Gargan, P.G., Vollset, K.W. et al. (2015) Effects of salmon lice *Lepeophtheirus salmonis* on wild sea trout *Salmo trutta* - a literature review. *Aquaculture Environment Interactions*, *7*, 91–113. <https://doi.org/10.3354/aei00142>
- Thorstad, E.B., Todd, C.D., Uglem, I., Bjørn, P.A., Gargan, P.G., Vollset, K.W. et al. (2016) Marine life of the sea trout. *Marine Biology*, *163*, 47. <https://doi.org/10.1007/s00227-016-2820-3>
- Tillotson, M.D. & Quinn, T.P. (2017) Climate and conspecific density trigger pre-spawning mortality in sockeye salmon (*Oncorhynchus nerka*). *Fisheries Research*, *188*, 138–148. <https://doi.org/10.1016/j.fishres.2016.12.013>
- Tummers, J.S., Hudson, S. & Lucas, M.C. (2016) Evaluating the effectiveness of restoring longitudinal connectivity for stream fish communities: towards a more holistic approach. *Science of the Total Environment*, *569*, 850–860. <https://doi.org/10.1016/j.scitotenv.2016.06.207>
- Turnpenny, A.W.H. & Williams, R. (1980) Effects of sedimentation on the gravels of an industrial river system. *Journal of Fish Biology*, *17*, 681–693. <https://doi.org/10.1111/j.1095-8649.1980.tb02802.x>
- UN/ECE. (1999) *Protocol to the 1979 convention on long-range transboundary air pollution to abate acidification, eutrophication, and ground-level ozone*. Geneva: United Nations Economic Commission for Europe. Available at: <http://www.unece.org/env/lrtap/protocol/>. [Accessed 12th Dec 2020].
- van Puijenbroek, P.J., Buijse, A.D., Kraak, M.H. & Verdonshot, P.F. (2019) Species and river specific effects of river fragmentation on European anadromous fish species. *River Research and Applications*, *35*, 68–77. <https://doi.org/10.1002/rra.3386>
- Vehanen, T., Huusko, A., Mäki-Petäys, A., Louhi, P., Mykrä, H. & Muotka, T. (2010b) Applied issues: effects of habitat rehabilitation on brown trout (*Salmo trutta*) in boreal forest streams. *Freshwater Biology*, *55*, 2200–2214. <https://doi.org/10.1111/j.1365-2427.2010.02467.x>
- Vehanen, T., Sutela, T. & Korhonen, H. (2010a) Environmental assessment of boreal rivers using fish data—a contribution to the Water Framework Directive. *Fisheries Management and Ecology*, *17*, 165–175. <https://doi.org/10.1111/j.1365-2400.2009.00716.x>
- Venus, T.E., Smialek, N., Pander, J., Harby, A. & Geist, J. (2020) Evaluating cost trade-offs between hydropower and fish passage mitigation. *Sustainability*, *12*, 8520. <https://doi.org/10.3390/su12208520>
- Verspoor, E. (1997) Genetic diversity among Atlantic salmon (*Salmo salar* L.) populations. *ICES Journal of Marine Science*, *54*, 965–973.
- Verspoor, E. & Cole, L.J. (2005) Genetic evidence for lacustrine spawning of the non-anadromous Atlantic salmon population of Little Gull Lake, Newfoundland. *Journal of Fish Biology*, *67*, 200–205. <https://doi.org/10.1111/j.0022-1112.2005.00848.x>
- Vosyliënė, M.Z. & Kazlauskienė, N. (2004) Comparative studies of sublethal effects of ammonia on rainbow trout (*Oncorhynchus mykiss*) at different stages of its development. *Acta Zoologica Lituonica*, *14*, 13–18. <https://doi.org/10.1080/13921657.2004.10512568>
- Walker, A.M. & Bayliss, B.D. (2007) The spawning habitat requirements of sea trout: a multi-scale approach. In: Harris, G. & Milner, N. (Eds.) *Sea trout biology, conservation & management*. Oxford: Blackwell Publishing Ltd.
- Wang, S., Hard, J.J. & Utter, F. (2002) Salmonid inbreeding: a review. *Reviews in Fish Biology and Fisheries*, *11*, 301–319. <https://doi.org/10.1023/A:1021330500365>
- Ward, J.V. (1989) The four-dimensional nature of lotic ecosystems. *Journal of the North American Benthological Society*, *8*, 2–8. <https://doi.org/10.2307/1467397>
- Ward, J.V. & Wiens, J.A. (2001) Ecotones of riverine ecosystems: Role and typology, spatio-temporal dynamics, and river regulation. *Ecology and Hydrobiology*, *1*, 25–36.
- Wauer, G., Heckemann, H.J. & Koschel, R. (2004) Analysis of toxic aluminium species in natural waters. *Microchimica Acta*, *146*, 149–154. <https://doi.org/10.1007/s00604-004-0198-2>
- Weatherley, N.S., Rogers, A.P., Goenaga, X. & Ormerod, S.J. (1990) The survival of early life stages of brown trout (*Salmo trutta* L.) in relation to aluminium speciation in upland Welsh streams. *Aquatic Toxicology*, *17*, 213–230.
- Weatherley, N.S., Thomas, S.P. & Ormerod, S.J. (1989) Chemical and biological effects of acid, aluminium, and lime additions to a Welsh hillstream. *Environmental Pollution*, *56*, 283–297.
- Webb, J. (1989) The movements of adult Atlantic salmon in the River Tay. *Scottish Fisheries Research Report*, *44*, 1–32.
- Webb, J.H., Gibbins, C.N., Moir, H. & Soulsby, C. (2001) Flow requirements of spawning Atlantic salmon in an upland stream: Implications for water-resource management. *Water and Environment Journal*, *15*, 1–8.
- Webb, J., Verspoor, E., Aubin-Horth, N., Romakkaniemi, A. & Amiro, P. (2007) The Atlantic salmon. In: Verspoor, E., Strandmeyer, L. & Nielsen, J.L. (Eds.) *The Atlantic salmon: genetics, conservation and management*. Oxford: Blackwell Publishing Ltd, pp. 18–45.
- Wedekind, C. & Mueller, R. (2005) Risk-induced early hatching in salmonids. *Ecology*, *86*, 2525–2529. <https://doi.org/10.1890/04-1738>
- Weiss, L.C., Pötter, L., Steiger, A., Kruppert, S., Frost, U. & Tollrian, R. (2018) Rising pCO<sub>2</sub> in freshwater ecosystems has the potential to negatively affect predator-induced defenses in *Daphnia*. *Current Biology*, *28*, 327–332. <https://doi.org/10.1016/j.cub.2017.12.022>
- Westley, P.A.H., Ings, D.W. & Fleming, I.A. (2011) A review and annotated bibliography of the impacts of invasive brown trout (*Salmo trutta*) on native salmonids, with an emphasis on Newfoundland waters. *Canadian Technical Reports on Fisheries and Aquatic Sciences*, *2924*, 81.
- Wilby, R.L., Orr, H.G., Hedger, M., Forrow, D. & Blackmore, M. (2006) Risks posed by climate change to the delivery of Water Framework Directive objectives in the UK. *Environmental International*, *32*, 1043–1055. <https://doi.org/10.1016/j.envint.2006.06.017>
- Williams, W.D. & Aladin, N.V. (1991) The Aral Sea: recent limnological changes and their conservation significance. *Aquatic Conservation*



- in *Marine and Freshwater Ecosystems*, 1, 3–23. <https://doi.org/10.1002/aqc.3270010103>
- Willson, M.F. & Halupka, K.C. (1995) Anadromous fish as keystone species in vertebrate communities. *Conservation Biology*, 9, 489–497. <https://doi.org/10.1046/j.1523-1739.1995.09030489.x>
- Witzel, L.D. & MacCrimmon, H.R. (1983) Embryo survival and alevin emergence of brook charr, *Salvelinus fontinalis*, and brown trout, *Salmo trutta*, relative to redd gravel composition. *Canadian Journal of Zoology*, 61, 1783–1792. <https://doi.org/10.1139/z83-230>
- Wolter, C. (2014) Historic catches, abundance, and decline of Atlantic salmon *Salmo salar* in the River Elbe. *Aquatic Sciences*, 77, 367–380. <https://doi.org/10.1007/s00027-014-0372-5>
- Wood, C.M. & McDonald, D.G. (1987) The physiology of acid aluminium stress in trout. *Annales de la Société Royale Zoologique de Belgique*, 117, 399–410.
- World Conservation Monitoring Centre. (1996) *Salmo salar*. The IUCN Red List of Threatened Species 1996: e.T19855A9026693. Available at: <https://doi.org/10.2305/IUCN.UK.1996.RLTS.T19855A9026693.en>. [Accessed 9 May 2021].
- Youngson, A.F., Knox, D. & Johnstone, R. (1992) Wild adult hybrids of *Salmo salar* L. and *Salmo trutta* L. *Journal of Fish Biology*, 40, 817–820. <https://doi.org/10.1111/j.1095-8649.1992.tb02628.x>
- Zimmermann, A.E. & Lapointe, M. (2005) Intergranular flow velocity through salmonid redds: sensitivity to fines infiltration from low intensity sediment transport events. *River Research and Applications*, 21, 865–881. <https://doi.org/10.1002/rra.856>

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