

This is an electronic reprint of the original article.

This reprint *may differ* from the original in pagination and typographic detail.

Author(s): Jan Heggenes, Morten Stickler, Knut Alfredsen, John E. Brittain, Ana Adeva-Bustos and Ari Huusko

Title: Hydropower-driven thermal changes, biological responses and mitigating measures in northern river systems

Year: 2021

Version: Published version

Copyright: The Author(s) 2021

Rights: CC BY-NC-ND 4.0

Rights url: <http://creativecommons.org/licenses/by-nc-nd/4.0/>

Please cite the original version:


Heggenes, J, Stickler, M, Alfredsen, K, Brittain, JE, Adeva-Bustos, A, Huusko, A. Hydropower-driven thermal changes, biological responses and mitigating measures in northern river systems. *River Res Applic.* 2021; 37: 743– 765. <https://doi.org/10.1002/rra.3788>

All material supplied via *Jukuri* is protected by copyright and other intellectual property rights. Duplication or sale, in electronic or print form, of any part of the repository collections is prohibited. Making electronic or print copies of the material is permitted only for your own personal use or for educational purposes. For other purposes, this article may be used in accordance with the publisher's terms. There may be differences between this version and the publisher's version. You are advised to cite the publisher's version.

REVIEW PAPER

WILEY

Hydropower-driven thermal changes, biological responses and mitigating measures in northern river systems

Jan Heggenes^{1,2}  | Morten Stickler^{1,3} | Knut Alfredsen⁴  | John E. Brittain^{2,3} | Ana Adeva-Bustos^{4,5}  | Ari Huusko⁶

¹Department of Natural Sciences and Environmental Health, University of South-Eastern Norway, Bø, Norway

²Natural History Museum, University of Oslo, Oslo, Norway

³Norwegian Water Resources & Energy Directorate, Oslo, Norway

⁴Department of Hydraulic and Environmental Engineering, Norwegian University of Science and Technology, Trondheim, Norway

⁵SINTEF Energy Research, Trondheim, Norway

⁶Natural Resources Institute Finland, Kainuu Fisheries Research Station, Paltamo, Finland

Correspondence

Jan Heggenes, Department of Natural Sciences and Environmental Health, University of South-Eastern Norway, Campus Bø, Gullbringvegen 36, 3800 Bø I Telemark Norway.

Email: jan.heggenes@usn.no

Funding information

Statkraft; University of South Eastern Norway

Abstract

Water temperatures control life histories and diversity of aquatic species. Hydropower regulation, particularly in high head systems, alters natural water temperature regimes, which may have profound and long-term impacts on aquatic environments. Temperatures in by-pass sections and reaches affected by residual/environmental minimum flows fluctuate more than in natural flow regimes, driven more by influence of air temperatures. Reaches downstream of power plant outlets tend to become warmer in winter and colder in summer, driven by stratification behind the reservoir dam. In hydro-peaked systems high-low temperature effects may thus be aggravated. We review alterations of hydropower to natural thermal regimes, impacts on key organisms in terms of survival, development and behavioral thresholds, and potential mitigation measures, with focus on Atlantic salmon and brown trout in high northern latitude stream systems. Previous syntheses have focused mainly on flow changes and ecological impacts. Temperature effects may not always be correlated with flow changes, although there are some unique challenges with temperature changes in far northern latitudes, for example, related to the seasonal and colder climates. To help knowledge-based management and identify potential knowledge gaps, we review how hydropower regulation may impact seasonal water temperatures, what impacts changes to stream system temperature regimes may have to key organisms, for example, Atlantic salmon and brown trout, and what adaptations and behavioral variations they may exhibit to respond to changed temperature regimes, and finally what good practices can be recommended for mitigating temperature impacts. This synthesis indicates that there are impacts to the fish and their supporting food webs, in particular related to growth and development, and the potential for negative impacts seems higher, and better studied, than positive impacts in northern river systems. Some of these impacts may be modified by directed hydropower regulation practices, but here effect studies and knowledge are limited.

KEYWORDS

biological impacts, hydropower regulation, mitigation, rivers, temperature

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2021 The Authors. *River Research and Applications* published by John Wiley & Sons Ltd.

1 | INTRODUCTION

Water temperature is a controlling factor in aquatic species' life cycle, growth, and diversity in lotic environments (e.g., Caissie, 2006; Gillespie, Desmet, Kay, Tillotson, & Brown, 2015; Hynes, 1970; Ward & Stanford, 1982; Webb & Walling, 1993). In northern cold climates, the balance between length and intensity of low and high temperature seasons (Peel, Finlayson, & McMahon, 2007) is pervasively important in aquatic lotic systems. This balance will be affected by the 21st century predicted climate change (e.g., Graham & Harrod, 2009; Heino, Erkinaro, Huusko, & Luoto, 2016; Jonsson & Jonsson, 2009). However, many of these small-intermediate stream systems are already affected by hydropower regulation and associated water temperature changes.

In such northern temperate streams extensively regulated for hydropower, environmental impacts are likely to be complex and site-specific (Gillespie et al., 2015; Poff & Zimmerman, 2010) and depend on spatial scale ("large" vs. "small" river systems, typically indicated by, for example, higher channel slope, smaller drainage area, higher relative roughness and shear stress, and more cascade, step-pool, plane bed habitat in 'small' river systems [Montgomery & Buffington, 1997]). A decrease in downstream inter-annual and intra-annual variability is typical for the hydropower regulated flow regime, notably for water flow and temperature (Geris, Tetzlaff, Seibert, Vis, & Soulsby, 2015; Renofalt, Jansson, & Nilsson, 2010; Ward & Stanford, 1979). Hydropower systems can typically be divided into high head systems comprising reservoirs at high elevation and long transfer tunnels to the power plant (Figure 1 top) and low head systems or run-of-the-river plants (Figure 1 bottom). With the limited

storage capacity in river reservoirs, low head hydropower regulation systems tend to have limited effects on stream water temperatures (Figure 1) (Asvall, 2008; Dickson, Carrivick, & Brown, 2012; Olden & Naiman, 2010). In contrast, with the large storage capacity in reservoirs, a high head system, common in northern river systems, may lead to major changes in water temperatures, in particular when there is a direct path from a high-altitude reservoir to a lowland river. Particularly in systems with large reservoirs, thermal regimes may be altered toward cooling in summer and warming in winter, including changes in ice formation, effected by the typical reservoir bottom intakes which tend to draw from the hypolimnion, where water temperatures are often stratified into a winter 'warm' layer and a summer cold layer (Figure 5). The impacts on aquatic life may be profound and long-term, potentially altering life histories and biological diversity.

Water temperature is, therefore, an important water quality indicator and parameter for potential mitigation measures aimed at restoring and managing water bodies. Recent reviews of ecological responses in regulated river systems have, however, focused more on the obvious direct impacts from flow changes (Gillespie et al., 2015; Olden et al., 2014; Poff & Zimmerman, 2010); (but see Austin, Bradley, Steward-Rousson, & Milner, 2015). Water temperature effects have attracted less attention, and it remains difficult to isolate the contributions of water temperature and water flow in biotic responses (Olden & Naiman, 2010), particularly in empirical studies (details in Heggenes, Alfredsen, Brittain, et al., 2017). We focus on temperature in this review, and with emphasis on the more numerous small-intermediate scale hydropower developments, because less synthesis of the impacts of water temperature changes on such systems has been provided.

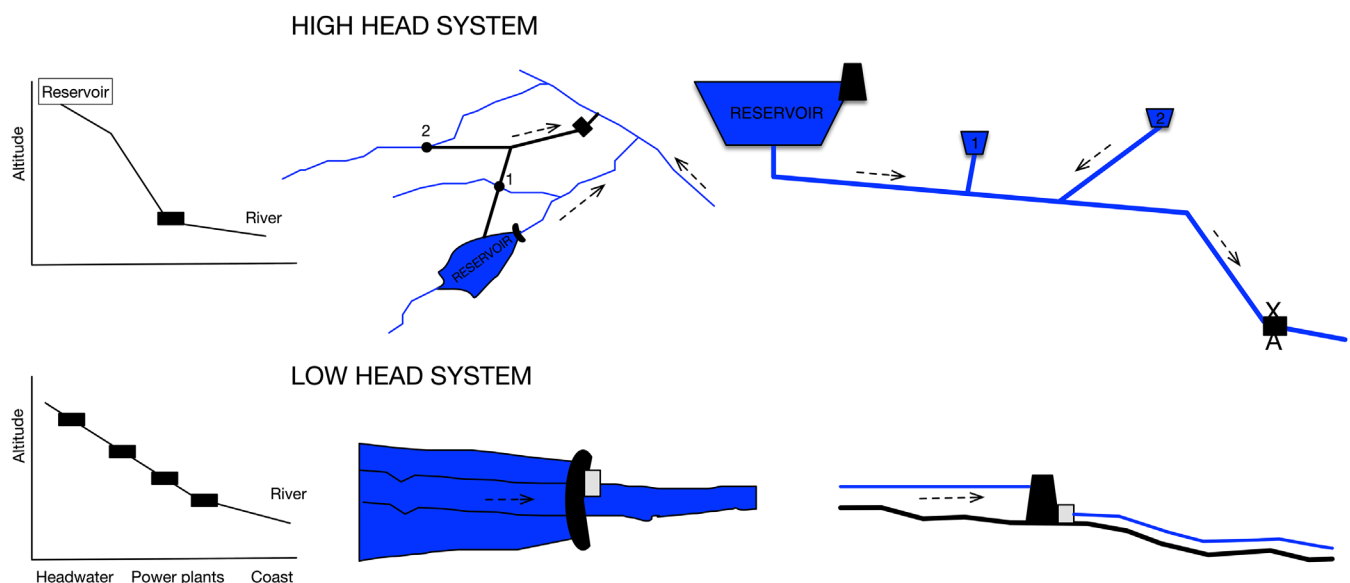


FIGURE 1 The two typical hydropower regulation systems. Top: a high head system with a high elevation reservoir, tributary intakes, and transfer tunnels to the power plant, which could also include a pumped storage facility. Bottom: a low head or run-of-the-river mainstem system with intake and power station in the river dam. Output from generation station equals input from the river upstream. (After Heggenes et al., 2017; Heggenes, Alfredsen, Bustos, Huusko, & Stickler, 2017; Toffolon, Siviglia, & Zolezzi, 2010) [Color figure can be viewed at wileyonlinelibrary.com]

In ectothermic freshwater animals, seasonal water temperatures may be the most pervasive environmental factor determining their lives (Angilletta, Steury, & Sears, 2004; Hynes, 1970). The rates of biochemical reactions, ontological development, and behavioral responses depend on water temperature (e.g., Angilletta, Niewiarowski, & Navas, 2002; Dell, Pawar, & Savage, 2011; Elliott & Elliott, 2010) and sublethal effects such as life history traits, egg development, and hatching cues. Temperature extremes, such as extraordinarily high summer or low winter temperatures, may generate short-term thermal stress and challenge physiological tolerances (Beitinger, Bennett, & McCauley, 2000; Elliott & Elliott, 2010; Gunderson & Stillman, 2015; Sunday et al., 2019). Thermal stress may be mitigated by basal thermo-tolerance or adaptive plastic responses involving acclimation and/or local behavioral adjustments (Gunderson & Stillman, 2015; Hutchison & Maness, 1979; Pörtner, 2002). In seasonal climates, long-term fitness may reflect the ability of ectothermic organisms to exploit the favorable summer season for temperature-dependent growth and recruitment. Developmental, physiological, and behavioral strategies may also mitigate the effects of the unfavorable low temperature season (Bradshaw, Zani, & Holzapfel, 2004; Hedger et al., 2013), which may include freezing ($\leq 0^{\circ}\text{C}$) and ice formation (Prowse, 2001; Turcotte & Morse, 2013).

In this review, we question how northern latitude hydropower regulation impact seasonal water temperatures in reaches downstream hydropower plants, including ice phenomena, and using Nordic river systems as a focus. How do impacted thermal regimes impact the ecology of selected key organisms, considering their survival thresholds, adaptations, and behavioral variations? And what potential mitigation measures could be applied to mitigate such impacts, and how effective are they? The widely distributed and both ecologically and culturally important fish species, Atlantic salmon (*Salmo salar* L.) and brown trout (*Salmo trutta* L.) are used as model fish species, but we also draw on results from other salmonid fishes, while benthic macroinvertebrates examples represent the lower trophic level supporting much of these species' production in lotic environments.

2 | HOW CAN HYDROPOWER REGULATION ALTER NATURAL THERMAL REGIMES?

Life in northern rivers has adapted to natural thermal regimes for millennia, before being disrupted by substantial hydropower development and associated thermal alterations only during the last hundred years or so.

2.1 | Water temperature processes in natural northern river systems

In northern environments, rivers exhibit seasonal variations in ambient temperatures. Water temperatures are low in winter, typically close to zero degrees with ice formation. This may determine survival. During

summer high temperatures determine growth and biological production. Within seasons, the thermal regime is largely controlled by temperatures in amount of water contributed from upstream lakes and reservoirs, tributaries, and groundwater (Figure 2). In addition, a watershed's heat radiation regime and subsoil environment, broadly determined by atmospheric conditions, topography, streambed, and stream discharge (Caissie, 2006), also affect water temperatures (Figure 2). Rivers per se typically heat or cool primarily by radiation to or from the surface (e.g., Caissie, 2006; Rishel, Lynch, & Corbett, 1982), but this may be modified by the surrounding environment, including the hyporheic zone (Caissie, 2006; Poole & Berman, 2001). Microgradients in stream temperature (cm to meters; Webb, Hannah, Moore, Brown, & Nobilis, 2008) tend to be limited, and if found, are related to strong solar heating and low flows, inflows from sources with different thermal characteristics, notably meltwater, groundwater, tributaries, lake outflows, and associated vegetation (e.g., Dugdale, Malcolm, Kantola, & Hannah, 2018; Nuhfer, Zorn, & Wills, 2017). Thus, thermal complexity in northern rivers may be considerable and may vary between day and night, particularly in small, alpine streams largely affected by short wave radiation and groundwater fluxes (Figure 2) (Brown, Hannah, & Milner, 2006; Cadbury, Hannah, Milner, Pearson, & Brown, 2008; Ward, 1994). On a temporal scale, diel, annual and interannual temperature variation tends to be more pronounced in smaller compared to larger streams (Figure 1). On a larger spatial scale, northern stream temperatures tend to increase with the lower altitudes downstream, but may be modified by for example groundwater and tributary inflows (Figure 2). In winter, sub-zero air temperatures may induce ice formation when water temperatures fall below zero, that is, supercooled water. Supercooled water occurs both on short temporal (minutes, hours) and spatial scales ($T_{\text{winter}}: -0.06 - -0.001^{\circ}\text{C}$) (Stickler & Alfredsen, 2009) and is therefore sensitive to even small changes in temperature.

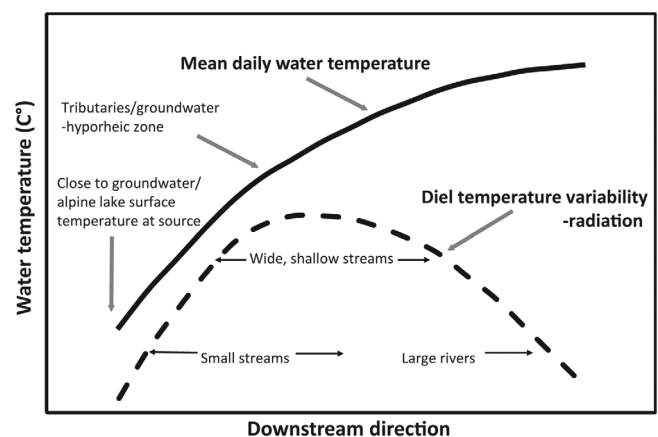


FIGURE 2 Schematic representation of mean daily and diel water temperature variability as a function of spatial scale, that is, downstream direction, which also generally translates to stream order. (Modified after Caissie, 2006; Austin et al., 2015)

2.2 | Hydropower regulation impacts on water temperatures in river systems

The extent of hydropower generated changes on the water temperature regime depends primarily on the hydropower regulation system, reservoir capacity, inflow and outflow valve position and capacity, and operational strategy, that is, origin, timing, and amount of water released for hydropower production (Archer, 2008; Hamblin & McAdam, 2003; Webb & Walling, 1997). Typically in high-head regulation systems, facilities draw reservoir water from the hypolimnion ("bottom layer") and transfer it directly to the power plant (Figures 1 & 5), bypassing downstream river reaches and leaving residual or environmental flows. Because water density is the highest around 4°C, temperature stratified reservoirs flip from warmest water in the hypolimnion (bottom layer) in the winter to coldest water on the bottom in summer. Therefore, in summer, the water downstream of hydropower outlet is cooled by release of hypolimnic water from the reservoir, but warmed in winter (Figures 3 & 4). In broad terms, this leads to reduced diurnal temperature fluctuations and changes in seasonal temperature regimes, notably winter warming and summer cooling (Figure 3 & 4) (Austin et al., 2015; Poff & Zimmerman, 2010; Poole & Berman, 2001), with associated important ecological effects, noting likely site-specificity and complexity. Unfortunately, the number of studies that quantify the water temperature (and chemistry) effects of dam-induced change are limited (Archer, 2008; Austin et al., 2015; Gillespie et al., 2015; Haxton & Findlay, 2008).

For northern streams, impacts of hydropower regulation on water temperature are neither well published nor quantified (Ellis & Jones, 2013) (but see e.g., Tvede, 1994; Kvambekk, 2004). In winter, the naturally near 0°C water temperatures and stable mid-winter periods with surface ice cover may be replaced by warmer water and repeated unstable transition periods in regulated systems (Figures 3 & 4) (Gebre, Alfredsen, Lia, Stickler, & Tesaker, 2013; Prowse et al., 2011; Stickler & Alfredsen, 2009; Weber, Nilsson, Lind, Alfredsen, & Polvi, 2013). Water drawn from the reservoir hypolimnion will in most cases raise downstream winter water temperatures above the natural level, from around 0° to maybe 2°C or more (Halleraker, Sundt, Alfredsen, & Dangelmaier, 2007; Ugedal et al., 2008) (Figure 3a & 4). Additional heat flux from transfer systems due to frictional heat from moving water in tunnels, may occur, but are expected to be limited, and local flow pressure changes may be more relevant (Ettema, Kirkil, & Daly, 2009). Importantly, release of warm water during winter may also alter downstream ice dynamics, even with relatively small water temperature changes (Asvall, 2008). The natural, typically stable mid-winter surface ice period may after regulation be replaced by prolonged unstable periods with dynamic ice formation and the absence of surface ice cover, exposing the river to frazil ice (Timalsina, Alfredsen, & Killingtveit, 2015; Timalsina, Charmasson, & Alfredsen, 2013; Ugedal et al., 2008). On the other hand, warm water releases may reduce the possibility of large ice runs (Gebre et al., 2013) due to periodic and controlled ice runs throughout the winter. Bypass river sections with reduced/required flow will experience higher water temperature variability during fall and spring

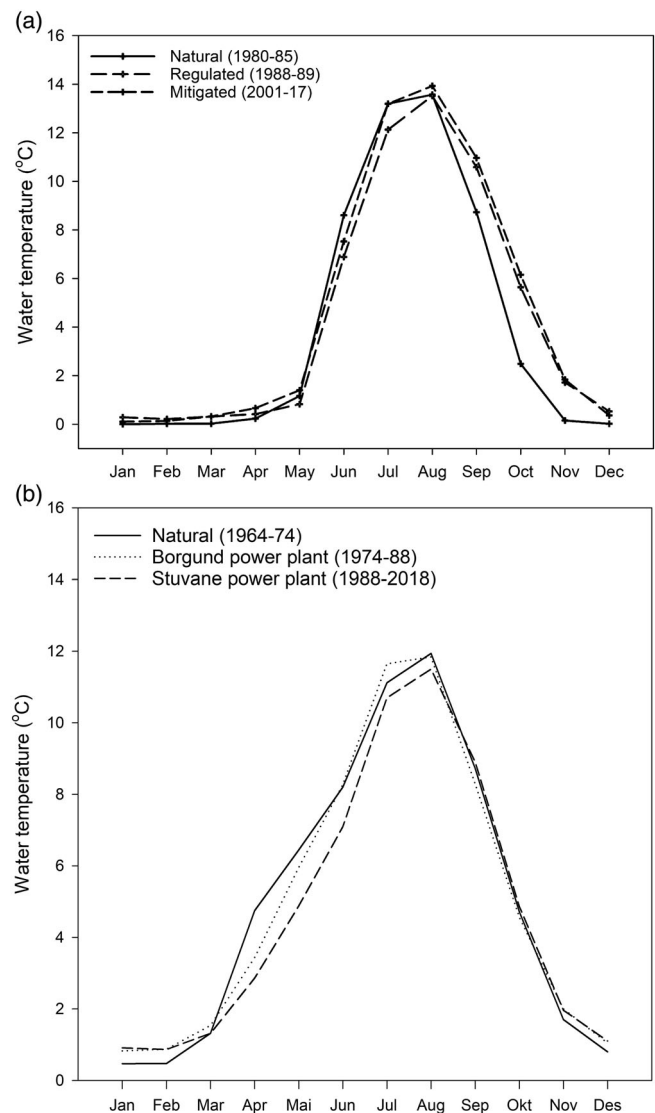


FIGURE 3 (a) Mean monthly water temperatures for Alta River, North-Norway, were raised 1–2°C primarily in fall–winter from before to after regulation. The effect was reduced somewhat after restoration/mitigation, primarily to obtain more surface ice cover in winter. (b) Mean monthly water temperatures for Lærdalselva River, West-Norway, were raised 1–2°C primarily in spring–summer from before to after regulation. (Data source: Norwegian Water and Energy Directorate)

and potentially more freezing in winter, but this may be modified particularly by groundwater flows (Asvall, 1977; Constantz, 1998; Osterkamp & Gosink, 1983). Unfortunately, most previous impact studies are rather qualitative, with little quantitative data on natural versus regulated temperature differences in winter, and effects of alternative production regimes (Austin et al., 2015; Olden & Naiman, 2010).

Drawing water from the reservoir hypolimnion and releasing it downstream of the hydropower plant may result in complex thermal and seasonal longitudinal effects (Tvede, 1994; Webb et al., 2008; Webb & Walling, 1997), largely depending on the balance between

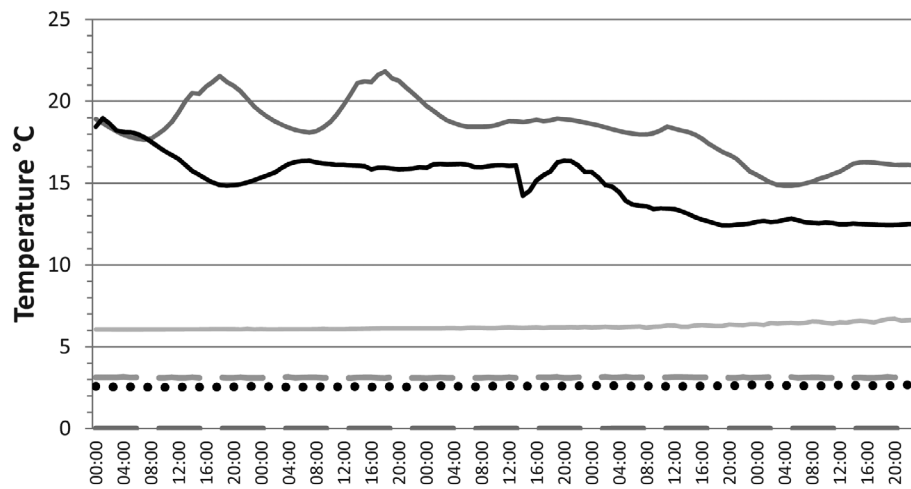


FIGURE 4 Typical winter (bottom dashed lines) and summer (top solid lines) water temperature changes effected by high head hydropower regulation (January and July 2009, Vallaråi R., South-East Norway). Winter: Upstream residual flow water with temperature about 0°C (lower dashed dark grey line) is mixed with hydropower reservoir water with temperature about 3.2°C from the station outlet (top dashed grey line), resulting in a downstream temperature of about 2.5°C (middle dotted black line). Summer: Upstream residual flow water with temperatures around 20°C (top solid dark grey line) is mixed with hydropower reservoir water with temperature about 13°C from the station outlet (lower solid grey line), resulting in a downstream reduction in temperature by about 5°C (middle solid black line)

residual and regulated flow. Although water temperature changes have been reported for tens of kilometers downstream or more in larger systems (Austin et al., 2015; Webb & Walling, 1993, 1988), for example, 10–60 km downstream a hydropower outlet (Archer, 2008; Ellis & Jones, 2013; Halleraker et al., 2007; Webb & Walling, 1988), more in situ studies are needed to determine the extent of impacts. Although models suggest thermal alterations due to hydropeaking/thermopeaking (Toffolon et al., 2010; Vanzo, Siviglia, Carolli, & Zolezzi, 2016), there are few studies that empirically illustrate such alterations (Bakken, King, & Alfredsen, 2016; Bruno, Siviglia, Carolli, & Maiolini, 2013; Casas-Mulet, Alfredsen, Brabrand, & Saltveit, 2015; Casas-Mulet, Alfredsen, Hamududu, & Timalisina, 2015). Empirical validations will be important in the future as short-term operational regimes are to be expected (e.g., Catrinu-Renström & Knudsen, 2011).

3 | IMPACTS OF ALTERED THERMAL REGIMES ON THE ECOLOGY OF KEY ORGANISMS

Low temperatures in northern climates are a controlling factor for production and natural selection for fish and macroinvertebrates (e.g., Elliott & Elliott, 2010; Huryn & Wallace, 2000; Ward, 1994). Responses to seasonal temperature variation constitute part of natural thermal strategies (e.g., Crozier & Hutchings, 2014; Danks, 2008; Olsson, 1981). The thermal regime may shape important ecological events at different trophic levels (e.g., Barneche & Allen, 2018; Woodward, Perkins, & Brown, 2010). Thus, the life histories of northern fish species like brown trout and Atlantic salmon are largely controlled by water temperature in terms of the basic life history characteristics of feeding and growth and survival, and certain life stages may be

particularly sensitive to the thermal regime, for example, egg and alevin development, and the associated timing of spawning migration and spawning itself (e.g., Solomon & Lightfoot, 2008) (Table 1). At a lower trophic level, benthic macroinvertebrate responses to temperature are variable and species specific, and with more pronounced life history adaptations compared to stream-living fish species (Bale & Hayward, 2010; Brittain, 1991; Dallas & Ross-Gillespie, 2015; Lencioni, 2004).

3.1 | Water temperatures and fish: Feeding, growth, and survival of Atlantic salmon and brown trout

Water temperature and food availability are key factors influencing growth and life history in salmon and trout in lotic environments (Table 1) (e.g., Budy et al., 2013; Forseth, Letcher, & Johansen, 2010; Logez & Pont, 2011). The summer period is the principal feeding and growing season for river fish (Elliott, 2009; Elliott & Elliott, 2010; Forseth, Hurley, Jensen, & Elliott, 2001). Winter necessitates energy saving and survival strategies, for example, quiescence, sheltering, nocturnal behavior, and starvation (Crozier & Hutchings, 2014; Heggenes, Alfredsen, Bustos, et al., 2017; Shuter, Finstad, Helland, Zweimuller, & Holker, 2012). Thus, in regulated systems, the modified temperature regime will directly affect fish growth and fitness (Tables 1–3). The build-up of larger fat reserves in summer and lower depletion rates in winter may, to some extent, compensate for longer winters in natural northern systems (e.g., Shuter et al., 2012). Indeed, juvenile northern Atlantic salmon populations show lower lipid-depletion rates during winter than southern populations, and storage lipid levels cluster close to critical

TABLE 1 An overview of thermal biology in the life histories of wild brown trout and Atlantic salmon

Life stage	Temperature effect	Brown trout	Atlantic salmon	Note	Selected references
Egg incubation period	Determined by degree-days (DD).	At 5°C ≈ 100 days. At 2°C ≈ 160 days.	At 5°C ≈ 100 days. At 2°C ≈ 160 days.	Varies somewhat with ambient temperature. Days to median hatch = $746 / (Temp - 0.5323)^{1.2233}$	Embody (1934), Jungwirth and Winkler (1984), Kane (1988). Formulae from Jungwirth and Winkler (1984)
Egg survival	Depends on temperature and oxygen level.	0–13°C Optimum at 8°C?	0–16°C Optimum at 6–8°C?	May increase if raised above 0°C. decrease markedly at higher temperatures. Suboptimal temperatures reduce alevin size. Low interpopulation variability. Some genetical adaptation?	Gunnes (1979), Reiser and Wesche (1979), Jungwirth and Winkler (1984), Stonecypher, Hubert, and Gern (1994); Ojanguren, Reyes-Gavilan, and Munoz (1999); Ojanguren and Brana (2003), Ornsrud, Gil, and Waagbo (2004), Ornsrud, Wargelius, Saele, Pittman, and Waagbo (2004), Takle, Baeverfjord, and Andersen (2004), Takle, Baeverfjord, Helland, Kjorsvik, and Andersen (2006), Syrjanen, Kiljunen, Karjalainen, Eloranta, and Muotka (2008)
Alevin development hatching to first feeding	Influenced by temperature, similar to eggs.	# of days = $193 T^{-0.83}$ ($r^2 = .970$). At 7.5°C ≈ 100 days.	# of days = $472 T^{-1.27}$ ($r^2 = .956$). At 7.5°C ≈ 100 days.		Kane (1988), Jensen, Johnsen, and Saksgard (1989), Ojanguren and Brana (2003)
Alevin survival	Depends on temperature.		<22°C	Survive higher temperatures than eggs. Lower survival during low temperatures and high flows.	Jensen and Johnsen (1999), Ojanguren et al. (1999), Syrjanen et al. (2008)
Fry to adult feeding	Temperature dependent activity.	4–18°C	4–22°C	Depends on acclimation. Indications of genetic adaptation.	Elliott, Hurley, and Fryer (1995), Elliott and Hurley (1997), Solomon and Lightfoot (2008)
Growth	Determined by temperature and food ration.	$G_W = cW_t^{-b} (T - T_{lim}) / (T_M - T)$	$G_W = cW_t^{-b} (T - T_{lim}) / (T_M - T)$	Interpopulation variation. Genetic adaptation?	Jensen (1990), Forseth and Jonsson (1994), Elliott et al. (1995), Elliott and Hurley (1997), Lobon-Cervia and Rincon (1998), Elliott and Elliott (2010)
Maximum growth		≈13°C	≈16°C	Interpopulation variation. Genetic adaptation?	Above

TABLE 1 (Continued)

Life stage	Temperature effect	Brown trout	Atlantic salmon	Note	Selected references
Avoided temperatures	Cease feeding and growth, induce thermal stress.	<3–4°C and >19–20°C at acclimation 15°C.	<5–6°C <6°C and >22°C at acclimation 15°C.	Depends on acclimation, few data for Atlantic salmon.	Elliott (1981), Elliott (1994), Elliott and Hurley (1997), Elliott and Elliott (2010)
7 days lethal temperature	Mortality.	≈25°C	≈28°C	Influenced by acclimation. Genetical adaptation?	Above
Smolt age	Temperature via growth/size.			Depends primarily on fish size. Influenced by several factors, including temperature.	Metcalf and Thorpe (1990), Saltveit (1990), Jonsson and Labée-Lund (1993)
Development of smolt characteristic	Primarily photoperiod, influenced by temperature.		Restricted <3°C, faster with increasing temperature (up to 10°C, and more?)		Staurnes, Sigholt, and Gulseth (1994), McCormick, Hansen, Quinn, and Saunders (1998)
Smolt migration	Several factors (e.g., flow, photo-period), including temperature.	Lower trigger temperature (≈ 7°C), less temperature dependent?	Triggered ≈ 10°C?	Interpopulation variation re. Factor importance. Genetic adaptation?	Hansen and Jonsson (1985), Jonsson and Ruud-Hansen (1985), McCormick et al. (1998), Byrne, Poole, Dillane, Rogan, and Whelan (2004), Stewart, Middlemas, and Youngson (2006), Solomon and Lightfoot (2008), Otero et al. (2014)
Swimming ability (burst swimming)	Limited by low temperatures.	Much reduced <≈5°C, in particular for smaller fish.	Much reduced <≈5°C, in particular for smaller fish.		Beamish (1979), Beach (1984)
Spawning migration	Several factors (e.g., flow), including temperature.		Reduced <≈5°C and >≈16°C, very little >20–23°C.		Juanes, Gephard, and Beland (2004), Solomon and Sambrook (2004), Saraniemi, Huusko, and Tahkola (2008), Quinn, McGinnity, and Reed (2016)
Gamete quality	Reduced by high temperatures.	??	>≈18°C	High temperatures reduce egg size, fertility and viability, certain time periods more sensitive.	King, Pankhurst, Watts, and Pankhurst (2003), Anderson, Swanson, Pankhurst, King, and Elizur (2012)
Ovulation	Reduced by high temperatures.		>14–16°C	Low temperatures (<7–3°C) may increase embryo survival.	Vikingstad et al. (2008), Vikingstad et al. (2016)
Spawning time	Temperature link via DD/egg development.		1–8°C	Timed to optimize early survival (above), much	Webb and McLay (1996), Shields, Stubbing, Summers, and

(Continues)

TABLE 1 (Continued)

Life stage	Temperature effect	Brown trout	Atlantic salmon	Note	Selected references
				interpopulation variation. Genetic adaptation?	Giles (2005), Jonsson and Jonsson (2009)
Spawning	Limited temperature range.		1–8°C? <11.5°C		Webb and McLay (1996), Solomon and Lightfoot (2008)
Thermal stress limits restricting long term population survival	High temperatures.	>19.5°C	>22.5°C	Regular occurrence of high temperatures causing thermal stress.	Solomon and Lightfoot (2008)

Note: Question marks denote uncertainty about temperature range given. (Adapted from Solomon & Lightfoot, 2008).

TABLE 2 Temperature tolerances (°C) for survival of Atlantic salmon and brown trout

Life stage	Atlantic salmon		Brown trout	
	Lower	Upper	Lower	Upper
Eggs	0	16	0	13
Alevins				
Long term ^a	0–2	23–24	0–1	20–22
Short term ^b	0–1	24–25	0	22–24
Parr and smolt				
Incipient	0–2	22–28	0–0.7	22–25
Ultimate	–0.8	30–33	–0.8	26–30
Feeding	0–7	22–28	0.4–4	19–26

Note: (After Elliott & Elliott, 2010).

^aIncipient Lethal Temperature (ILT): Tolerance for a long time period, usually 7 days.

^bUltimate Lethal Temperature (ULT): Tolerance for a short time period, usually 10 min.

Species	Lower	Upper	Optimum	Growth efficiency
Atlantic salmon				
UK	6.0	22.5	15.9	c. 13
Norway	1.0–7.7	23.3–26.7	16.3–20.0	12–18
Brown trout				
Invertebrate food	2.9–3.6	18.2–19.5	13.1–14.1	8.9
Fish food	c. 2.0	c. 19.5	16.6–17.4	9.3
Pelleted food	1.2–6.1	19.4–26.8	11.6–19.1	

Note: (After Elliott & Elliott, 2010).

TABLE 3 Temperature limits (°C) for growth range, optimum growth (on maximum rations), and maximum growth efficiency for Atlantic salmon and brown trout

limits for survival (Finstad, Berg, Forseth, Ugedal, & Naesje, 2010). Thus, Atlantic salmon and brown trout tend to exhibit a temperature dependent north–south gradient in winter lipid storage (Berg et al., 2009; Berg, Rod, Solem, & Finstad, 2011). Northern populations may also show a stronger positive scaling of feeding activity with decreasing energy levels, that is, presumably compensatory adaptive differences in state-dependent feeding motivation (Finstad et al., 2010). This may explain the observed variation in

lower temperatures for feeding activity in Atlantic salmon and brown trout (Tables 2 & 3). Temperature-dependent tolerances and changes in performance for Atlantic salmon and brown trout are well established in general (Tables 2 & 3) (Elliott, 1994; Fry, 1971; Larsson & Berglund, 2006). There is, however, also substantial thermal plasticity to be considered, and less is known about possible adaptations, both important with respect to potential responses to thermal regimes altered by hydropower.

TABLE 4 Summary of hydropower regulation water temperature impacts on life stages of brown trout and Atlantic salmon, with likely biological responses, ecological consequences, and potential mitigation measures

Life stage	(Potential) Temperature regulation impact	(Potential) Biological response	Ecological consequences	Potential mitigation measures
Egg incubation period	Determined by degree-days (DD). Warmer winter water shortens incubation period.	Earlier hatching, later spawning.	Mismatch of hatching with environmental conditions (flow, temperature, food availability).***	Reduce winter water temperatures via flexible water intakes and adaptive flow regime.
Egg survival	Depends on temperature. Regulation changes typically within egg survival temperature range. Changed ice phenomena may influence survival.	? Does a temperature increase for example, 0 → 3°C affect egg survival? Or changed ice phenomena?	? Changed population recruitment?*	Reestablish surface ice during winter via lower water temperatures via flexible water intakes and adaptive flow regime? Increase egg survival via stable flow of 2–3°C water, avoiding ice phenomena?
Alevin development, hatching to first feeding	Influenced by temperature, similar to eggs. Slower spring warming. (but also unpredictable transient temperatures).	Slower alevin development, smaller alevins.	Mismatch of alevin development with environmental conditions, for example, natural spring flows, food availability. Shorter growing season.***	Reduce regulated spring flow. Increase spring water temperatures via flexible water intakes and adaptive flow regime.
Alevin survival	Depends on temperature. Slower spring warming.	Lower survival during low temperatures and high flows. Prolonged alevin stage and reduced size lead to reduced survival?	Reduced population recruitment?*	Higher spring temperatures via flexible water intakes and adaptive flow regime.
Fry to SMOLT/adult feeding	Temperature dependent activity and metabolism. Slower spring warming, lower summer temperatures.	Typically reduced feeding. Potentially increased daytime feeding during summer in warm, wide-shallow streams receiving high solar radiation.	Lower production. Lower juvenile survival.*	Higher spring and early summer temperatures via flexible water intakes and adaptive flow regime. Avoid high summer temperatures via drawing cooler reservoir water.
Growth	Determined by temperature and food ration. Slower spring warming, lower summer temperatures.	Reduced growth. During high summer in warmer climates, growth may increase.	Smaller fish. Lower production.*** Lower juvenile survival.**	Higher summer temperatures via flexible water intakes and adaptive flow regime. Avoid high summer temperatures via drawing cooler reservoir water.
Maximum growth		≈ 13–16°C		Suitable summer temperatures via flexible water intakes and adaptive flow regime.
Avoided temperatures	Cease feeding and growth, induce thermal stress. Stabilize temperatures within suitable temperature range.	<3–6°C and >19–22°C at acclimation 15°C.	Reduced growth and lower survival**	
Smolt migration	Several factors (e.g., flow, photoperiod), including temperature. Slower spring warming.	Lower trigger temperature (≈ 7–10°C). Delayed smolt migration?	Lower ocean survival? Reduced population recruitment?*	Increase spring water temperatures via flexible water intakes and adaptive flow regime.
Spawning migration	Several factors (e.g., flow), including temperature. Higher early fall temperatures.	Delayed?	Delayed?*	

(Continues)

TABLE 4 (Continued)

Life stage	(Potential) Temperature regulation impact	(Potential) Biological response	Ecological consequences	Potential mitigation measures
Spawning time	Temperature link via DD/egg development. Warmer winter water shorten incubation period.	1–8°C. Later spawning.	?* See egg incubation	Timed to optimize early survival in natural streams.

Note: Question marks indicate knowledge gaps and important research areas. Effects will depend on local conditions and ramping regime. Increasing number of asterisks indicate increasing level of authors' confidence.

TABLE 5 Suggested future water temperature and hydropower regulation research and knowledge needs

Hydro-physical conditions

Seasonal and thermal longitudinal effects are neither well studied nor quantified. How extensive are they, and what local conditions (e.g., groundwater, tributaries, catchment run of) affect the changes?

How do different production regimes (e.g., peaking or seasonal) affect longitudinal downstream water temperatures?

Replacement of the naturally stable mid-winter surface ice period with prolonged transition periods may lead to more frazil ice formation and correspondingly unstable or no surface ice. This may expose fish and macroinvertebrates to more open water and frazil ice, but also to increased winter temperatures. How does this affect fish and macroinvertebrates?

To what extent do different macroinvertebrates survive encasement in ice?

Is egg survival and invertebrate production higher in "winter-warm" regulated rivers than in the natural state?

In regulated rivers, mechanistic ice breakup may occur several times and at any time during winter. To what extent does this cause higher winter mortality in fish?

Biological responses

Longitudinal water temperature impacts on fish populations and invertebrate communities at the river scale?

To what extent are there differences in both warm and cold water thermal performance among salmon and trout populations, and are such differences indicative of local thermal adaptations?

Mitigating measures

Have restored/increased flows in regulated rivers resulted in higher and/or more natural salmonid production? Also, has higher minimum discharge in winter after hydropower regulation, with associated higher water temperatures, resulted in higher parr survival rates and smolt production?

What are the effects of hydropower regulation-induced temperature changes/increases in early spring on egg and alevin development and survival?

A suite of numerical models for water temperature calculations in combination with models of effects on changing physical and thermal habitat on fish is available. There is, however, a scarcity of empirical examples?

Regarding models, development and integration of small-scale thermal (fish) habitat models and validation against fish data, are also remaining challenges.

3.1.1 | Thermal plasticity, but little adaptation

Variation in thermal tolerance throughout an Atlantic salmon or brown trout life cycle may be substantial and depends on developmental stage (Tables 1–3). The egg stage has the narrowest temperature tolerance (Table 2) (Elliott & Elliott, 2010), and the young-of-the-year, including the yolk sac stage, are less tolerant than later life stages (Ayllon, Nicola, Elvira, Parra, & Almodovar, 2013; Breau, Cunjak, & Peake, 2011; Elliott & Elliott, 2010). Atlantic salmon has generally greater tolerance of high water temperatures in all life cycle stages compared to brown trout, whereas brown trout is slightly more cold adapted (Table 2). Interestingly, temperature tolerances remain similar over a wide geographical range with negligible indications of regional adaptations (Elliott & Elliott, 2010), suggesting that observed variation in performance limits (Table 3) is primarily due to substantial phenotypic plasticity. Such plasticity enhance ecological resilience to thermal stress effected by hydropower development (Tables 4 & 5).

Feeding and growth in northern populations appear to some extent to be adapted to the longer and more intense winters. A northern Atlantic salmon population fed and grew better under the ice in the dark than their southern cousins, under benign laboratory tank conditions (Finstad, Forseth, Faenstad, & Ugedal, 2004; Finstad, Naesje, & Forseth, 2004). They in turn, grew better in the light without surface ice (Finstad & Forseth, 2006). This is important per se as hydropower may reduce surface ice formation, and this should therefore be more explored also outside the laboratory. Trout appear to grow better than expected in colder rivers (Jensen, Forseth, & Johnsen, 2000), suggesting adaptations. In species like Atlantic salmon and brown trout with a wide geographical distribution, and constraints on gene flow imposed by watershed isolation and restricted spatial dimensionality, intra-specific variation together with local adaptation, may be expected. Indeed, differences in warm and cold-water thermal performance exist among Atlantic salmon and brown trout populations (Anttila et al., 2013; Forseth et al., 2009; Hartman & Porto, 2014). However, whereas intraspecific phenotypic plasticity is important in providing ecological resilience, there is little indication of local thermal adaptation (Finstad & Jonsson, 2012; Jensen et al., 2008; Meier et al., 2014; Skoglund, Einum, Forseth, & Barlaup, 2011). This may seem surprising, but adaptations of enzyme systems to different temperatures appear to come at a high cost

(Portner, 2006; Shuter et al., 2012). In a few cases, there appear to be some genetically based local adaptation to winter climates, notably energy storage (Alvarez, Cano, & Nicieza, 2006; Berg et al., 2011; Crespel, Bernatchez, Garant, & Audet, 2013; Finstad et al., 2010). The maximum growth capacity in brown trout and Atlantic salmon may vary among populations, but neither correlate with local natural temperature optima nor indicate counter gradient variation in growth (Baerum, Vollestad, Kiffney, Remy, & Haugen, 2016; Forseth et al., 2009; Jonsson, Forseth, Jensen, & Naesje, 2001; Larsson & Berglund, 2006). Instead, adaptive variation in growth potential may be related to factors affecting reproductive success (Elliott & Elliott, 2010; Forseth et al., 2009; Jonsson & Jonsson, 2009). It has been suggested that thermal adaptations may occur as counter gradient adaptations in (very) cold environments (Elliott & Elliott, 2010; Finstad, Naesje, & Forseth, 2004; Jensen et al., 2000; Nicola & Almodovar, 2004), which would, in case, be particularly important in northern rivers influenced by hydropower development (Tables 4 & 5). Limited local thermal adaptation in Atlantic salmon has tentatively been attributed to the fact that they experience a common thermal environment in the North Atlantic Ocean which may perhaps be more important than freshwater growth in locally different temperature regimes (Forseth et al., 2009). For the more resident brown trout, different population-specific thermal regimes throughout its life history are more likely, in particular in colder streams (Alvarez et al., 2006; Jensen et al., 2000; Nicola & Almodovar, 2004), although environmental variability may account for most of the observed variation in annual growth rates.

Thus, salmonid species appear to be physiologically bound for optimal performance and growth to a rather specific range of summer temperatures (Tables 2 & 3) (Clarke & Portner, 2010; Shuter et al., 2012). The notion of “species-specific preferred temperature” $\pm 2^{\circ}\text{C}$ seems to work quite well (Magnuson, Crowder, & Medvick, 1979), although the optimal growth and preferred water temperature may be shifted toward the upper end of this window (Portner, 2010; Shuter et al., 2012). This “fundamental thermal niche” may explain population productivity and northern zoogeographic boundaries (Shuter et al., 2012). Interestingly, most freshwater fish, including the cold-water Atlantic salmon and brown trout, have preferred temperatures well above $4\text{--}5^{\circ}\text{C}$ (Tables 2 & 3) (Elliott & Elliott, 2010; Shuter et al., 2012), whereas ambient winter temperatures are well below that. On a cautionary note, optimum growth temperature decreases with decreasing energy intake (Elliott & Elliott, 2010). Therefore, optimum temperatures in nature may be lower than values reported in Table 3, which in part are based on maximum rations in the laboratory.

Consequently, even apparently moderate changes in natural water temperatures caused by hydropower regulation (e.g., Figure 1, Table 4) may have important effects on Atlantic salmon and brown trout growth and performance (Tables 1 & 4). Temperature is the most important factor in their growth models. Although originally based on relatively benign laboratory conditions with maximum rations, they may be good approximations of growth patterns in natural streams, demonstrating the importance of temperature (Elliott &

Elliott, 2010; Elliott & Hurley, 1997; Forseth et al., 2001; Jonsson et al., 2001). On a cautionary note, if growth during (early) summer is hampered for some reason, for example, by limited habitat during low flows and droughts, trout are capable of compensatory growth (Elliott, 2009, 2015), which may modify such models, and should therefore be explored more in a hydropower context in which change thermal regimes seasonally. Still, such growth models are robust with respect to assumed base growth temperatures (Chezik, Lester, & Venturelli, 2014) and are versatile tools that may be used in comparative studies (Hayes, 2013), for example, exploring potential fish production under alternative thermal regimes effected by different tapping and release strategies in a high-head hydropower system (Figure 1). Growth models may also be used to control for influence of other environmental factors, such as food availability (Sanchez-Hernandez, Gabler, Elliott, & Amundsen, 2016).

Foraging during low temperatures in winter is rare for salmon and trout, and winter is primarily about survival. The common strategy is energy storage (see review Heggenes, Alfredsen, Bustos, et al., 2017). Additional strategies are reduced metabolism, tolerance, and starvation effected by quiescence (Shuter et al., 2012) and shorter behavioral movements or migration to more suitable deep and slow flow winter habitat (Linnansaari et al., 2009; Rimmer, Paim, & Saunders, 1984; Saraniemi et al., 2008). Activity may result from lack of available refuge habitat and predation risk, but also easily available food, or perhaps stronger feeding motivation as energy stores become low (Heggenes, Alfredsen, Bustos, et al., 2017; Metcalfe, Fraser, & Burns, 1999). Brown trout may feed throughout the year, but little and with no apparent growth, or even shrinking, in winter (Elliott, 2009; Huusko, Maki-Petays, Stickler, & Mykra, 2011; Lien, 1978). Atlantic salmon and brown trout become less aggressive and less efficient foragers at lower light levels and temperatures (Elliott, 2011; Valdimarsson & Metcalfe, 2001). Downstream winter temperature warming due to river regulation tends to be in a range of $0\text{--}3^{\circ}\text{C}$ for high-head systems (e.g., Halleraker et al., 2007; Kvambekk, 2012). Such range is below the thermal thresholds for growth and foraging for Atlantic salmon and brown trout (Tables 1–3), suggesting that direct effects on growth may be limited.

3.1.2 | Autumnal fish migration, spawning, and egg development

For autumn spawning and downstream spring smolt migrations, the larger time window is regulated by photoperiod (McCormick et al., 1998; Moore et al., 2012; Robards & Quinn, 2002). However, water temperature and/or flow levels may control local migrations, although many other in situ factors may contribute (Table 1) (Cunjak, Linnansaari, & Caissie, 2013; Milner, Solomon, & Smith, 2012; Tetzlaff, Gibbins, Bacon, Youngson, & Soulsby, 2008; Thorstad, Okland, Aarestrup, & Heggberget, 2008). Spawning time appears to be population specific and locally adapted to winter temperature regimes targeting hatching and first feeding at the most opportune

time in spring (Jensen, Johnsen, & Heggberget, 1991; Shields et al., 2005). Thus, spawning is linked to autumnal water temperature (~ 1 – 6°C for peak spawning) (Jonsson & Jonsson, 2009; Riedl & Peter, 2013; Taranger & Hansen, 1993), with earlier spawning in colder rivers. Consequently, a modified winter thermal regime due to hydropower regulation is also likely to modify timing of spawning (Table 4). The duration of embryonic development primarily depends on the number of degree-days (DD) from spawning to hatching (Elliott & Hurley, 1998b; Embury, 1934; Jungwirth & Winkler, 1984; Kane, 1988). In brown trout DD is around 320 at low water temperatures of 2°C , but increasing to about 400 DD with increasing water temperatures up to 10°C . Post-regulation elevated winter water temperatures in regulated rivers will result in earlier hatching (Syrjanen et al., 2008) and may disrupt the delicate balance and link between timing of spawning (Jonsson & Jonsson, 2009; Shuter et al., 2012) and larval spring emergence. This timing maximizes growth performance the following summer season, but presumably also reduces mortality risk associated with spring runoff and wash-out of larvae (Einum & Fleming, 2000; Jensen et al., 1991; Jensen & Johnsen, 1999; Letcher et al., 2004; Skoglund, Einum, Forseth, & Barlaup, 2012).

Natural timing of emergence vary among years within a population, mainly due to variations in rapidly rising water temperatures in spring, and with spawning date as a secondary factor (Cunjak et al., 2013; Elliott & Elliott, 2010). The number of egg incubation DD may, like optimal growth temperature, show little adaptive variation, for example, among natural Atlantic salmon populations (Heggberget & Wallace, 1984; Wallace & Heggberget, 1988). Adaptation may rather be reflected in varying spawning times, but studies are limited with respect to population gradients investigated and results are somewhat ambiguous (Jonsson & Jonsson, 2009). Egg survival is typically high (Barlaup, Gabrielsen, Skoglund, & Wiers, 2008; Casas-Mulet, Saltveit, & Alfredsen, 2015; Elliott, 1994; Saltveit & Brabrand, 2013), but variable (Cunjak et al., 2013; Sear & DeVries, 2008) depending on a range of biotic and abiotic factors (Gibbins, Shellberg, Moir, & Soulsby, 2008; Greig, Sear, & Carling, 2007; Malcolm, Gibbins, Soulsby, Tetzlaff, & Moir, 2012; Saltveit & Brabrand, 2013; Stonecypher et al., 1994), including groundwater combined with local hyporheic environments and water temperatures. In the absence of groundwater with sufficient oxygen, egg mortality is likely to be higher with more shallow burial, that is, more exposure to dewatering and sub-zero temperatures (Casas-Mulet, Alfredsen, Brabrand, & Saltveit, 2015; Casas-Mulet, Alfredsen, Hamududu, & Timalsina, 2015; Casas-Mulet, Saltveit, & Alfredsen, 2015), an important consideration in regulated rivers and winter temperatures and flow (Tables 4 & 5). Altered thermal regimes linked to low flows may be a particular challenge. Increased temperatures due to regulation in winter may be a driver for early hatching, but translate into increased mortality if hatching occurs prior to the spring floods in areas of the river where redds are not fully covered with water. If hatching occurred later, eggs would survive, but not the alevins (Casas-Mulet, Alfredsen, Brabrand, & Saltveit, 2016; Casas-Mulet, Saltveit, & Alfredsen, 2016; Vanzo, Tancon, Zolezzi, Alfredsen, & Siviglia, 2016).

3.1.3 | Spring emergence and early mortality

The early stage related to the alevin emergence is an important regulatory period with natural high mortality in salmonid populations (Table 1) (Bret, Bergerot, Capra, Gouraud, & Lamouroux, 2016; Jonsson & Jonsson, 2009; Milner et al., 2003), at least in more benign, temperate streams, and high-density populations (Elliott, 2009; Jonsson, Jonsson, & Hansen, 1998) where competition for space and density-dependent mortality is important. Dominance is determined by size and aggressiveness, and the more aggressive brown trout dominates even larger Atlantic salmon (Einum & Fleming, 2000; Einum, Robertsen, Nislow, McKelvey, & Armstrong, 2011; Skoglund et al., 2012). Smaller individuals may be forced to move (Einum et al., 2012) incurring potentially high mortalities (Einum & Fleming, 2000; Elliott, 1994). In low-density (below carrying capacity) populations in more challenging environments, density-independent abiotic regulating factors such as flow and temperature may be more important (Bret et al., 2016; Cunjak et al., 2013; Elliott & Hurley, 1998a; Elliott, 1989; Lobon-Cervia & Mortensen, 2005; Lobon-Cervia, 2014). Higher temperatures may benefit survival, but not extreme temperatures (Gibson & Myers, 1988). Correspondingly, low water temperatures may negatively affect survival (Elliott, 1985; Jensen & Johnsen, 1999), especially combined with high flows (Bret et al., 2016). Experimental studies on brown trout and Atlantic salmon indicate that low incubation temperatures produce smaller fry with larger yolk sacs, relative to higher incubation temperatures (Skoglund et al., 2011; Syrjanen et al., 2008). The experimental fry started active feeding with growth even at the lowest temperatures of 2°C , and increasing with temperature, but temperature at first feeding is likely higher in nature, for example, 8°C for Atlantic salmon (Jensen et al., 1991). Smaller size or larger energy reserves may be beneficial under low spring temperature conditions because they may lower activity, which in turn increases sheltering and enables more cryptic feeding strategies. Alternatively, larger size resulting from warmer incubation temperatures may confer a competitive advantage. Thus, this should be explored in natura if increased downstream temperatures in winter typical of northern high-head hydropower regulation (above), do indeed result in larger fry with smaller yolk sacs (Tables 4 & 5).

3.2 | Water temperatures and the supporting food web: Macroinvertebrates

For benthic macroinvertebrates as a group, different species show considerable morphological and ecological variation, permitting adaptation to a wide range of aquatic thermal environments as well as notably widespread species with flexible life cycle length (Brittain, 1991; Brittain & Saltveit, 1989; Raddum & Fjellheim, 1993). Abiotic factors such as temperature, habitat, and water chemistry affect benthic macroinvertebrate development and production (Huryn & Wallace, 2000). Like for fish, seasonally low temperatures, in addition to food limitation, rather than specific modes of feeding or

life-history attributes, constrain macroinvertebrate production, which is lowest in cool-temperate and arctic streams (Huryn & Wallace, 2000).

Benthic macroinvertebrates use diverse winter strategies to cope with and even take advantage of winter conditions. Many species undergo cold-tolerant quiescence or diapause, most commonly in the egg stage (Brittain, 1990; Danks, 2008; Harper & Hynes, 1970; Lencioni, 2004), and this is usually cued by photoperiod. Movement, into the substrate/hyporheic or tributaries/deeper water, is a freeze avoiding strategy, which can be coupled with diapause/quiescence (Bale & Hayward, 2010; Lencioni, 2004; Olsson, 1981, 1983). Alternatively, certain species (Diptera, Plecoptera) stay-put and display freezing tolerance (Bale & Hayward, 2010; Lencioni, 2004; Lillehammer, 1987). Still, severe winters may reduce, at least in the short term, both benthic abundance and taxonomic richness (Hoffsten, 2003), and the majority of insects die from the effects of cold water rather than freezing (Bale & Hayward, 2010). This has important implications for vulnerability to winter warming in regulated rivers.

Modified water temperatures, for example, by hydropower regulation, may have major effects on normal rates of development and life cycles, as many facets of growth and emergence are affected and even cued by water temperature (Brittain, 1982; Dallas & Ross-Gillespie, 2015; Lillehammer, Brittain, Saltveit, & Nielsen, 1989; Raddum, 1985), also in the Southern Hemisphere (Dallas & Ross-Gillespie, 2015; Ross-Gillespie, Picker, Dallas, & Day, 2018). This facilitates modeling of potential impacts (Rivers-Moore, Dallas, & Ross-Gillespie, 2013). Moreover, since photoperiod is the dominant diapause-inducing cue and unaffected by hydropower regulation, unless the surface ice cover is changed, a modified temperature regime may lead to decoupling of synchrony between diapause-sensitive life stages and thermally challenging environments. Univoltine and longer life cycles are most at risk, while flexible, short life cycles will be favored (Brittain, 1991; Petrin, Brittain, & Saltveit, 2013). A reduction in the temperature range between winter and summer will lead to a reduction in species diversity (Vannote & Sweeney, 1980), again favoring the widespread, ubiquitous species (Brittain, 1991; Saltveit, Bremnes, & Brittain, 1994; Saltveit, Brittain, & Lillehammer, 1987). Reduced snow and ice cover, which may result from hydropower regulation, may expose macroinvertebrates to the more severe consequences of low air temperatures (Raddum, 1985), and increased frequency of freeze-thaw cycles may increase risks of ice encasement (Bale & Hayward, 2010). Frazil ice events, which may increase after hydropower regulation, may increase post-event drift (Martin, Brown, Barton, & Power, 2001; Sertic Peric & Robinson, 2015), and supercooled water may reduce macroinvertebrate abundance (Hoffsten, 2003; Martin et al., 2001), although benthic organisms may also survive entrapment in anchor ice (Brown, Clothier, & Alvord, 1953; Benson, 1955; Oswood, Miller, & Irons, 1991; Irons, Miller, & Oswood, 1993; but see Frisbie & Lee, 1997). The scarcity of Ephemeroptera and Plecoptera in frozen substrates suggests that these taxa either remain in habitats that do not freeze or move to

deeper water (Olsson, 1983; Oswood et al., 1991). Although most aquatic insects emerge during the ice-free period, some species emerge during winter, for example, in Chironomidae, Trichoptera, and Plecoptera (Brinck, 1949; Hågvar & Østbye, 1973; Lencioni, 2004).

During winter, allochthonous organic plant material (leaf litter) provides food utilized by winter growing shredder species (Brittain, 1983; Haapala & Muotka, 1998; Lillehammer et al., 1989), raising their abundance in winter (Haapala, Muotka, & Markkola, 2001). However, results are ambiguous, and winter reductions are also reported (Clifford, 1972; Martin et al., 2001; Morin, Rodriguez, & Nadon, 1995), perhaps because of reduced water flow (Waringer, 1992), reduced invertebrate activity (Ferreira & Canhoto, 2014; Martin et al., 2001), or increased food availability in the hyporheic zone (Dekar, Magoulick, & Huxel, 2009; Haapala & Muotka, 1998; Hildebrand, 1974; Vannote, Minshall, Cummins, Sedell, & Cushing, 1980). In general, mechanical disruption of the substrate, for example, by ice in winter, may dislodge benthic invertebrates (Butler & Hawthorne, 1979) and lead to increased downstream drift (Brittain & Eikeland, 1988; Finni & Chandler, 1979) and even faunal depletion in some cases (Colbo, 1979), although not in others (Brown et al., 1953).

We suggest that increased downstream winter temperatures may lead to increased growth rates in some macroinvertebrates (Table 5) (Nebeker, 1971; Raddum & Fjellheim, 1993; Raddum, Fjellheim, & Velle, 2008; Ward & Stanford, 1982), as growth and development in macroinvertebrates may continue in many species even at low winter temperatures (Huryn & Wallace, 2000; Svensson, 1966; Vannote & Sweeney, 1980), even in extreme Arctic environments that do not freeze solid (e.g., Coulson et al., 2014). Potentially higher invertebrate production in winter-warmer regulated rivers may precipitate more opportunistic feeding in fish and a potentially earlier start of the growth season. Unfortunately, such beneficial effects are not well studied (Table 5) and may be confounded with simultaneous changes in summer temperature and flow regime (Bruno et al., 2013; Bruno, Maiolini, Carolli, & Silveri, 2009; Cereghino, Cugny, & Lavandier, 2002; Jackson, Gibbins, & Soulsby, 2007; Miller & Judson, 2014).

4 | WHAT GOOD PRACTICES CAN BE RECOMMENDED FOR MITIGATING TEMPERATURE IMPACTS?

Hydropower regulation may increase downstream winter water temperatures up to 2–3°C or more, and mitigation measures reduce regulated winter water temperatures by perhaps 0.1–1°C (Halleraker et al., 2007; Kvambekk, 2012). Mitigation measures may increase summer temperatures by 0.1–2°C (Halleraker et al., 2007). However, the mitigation potential may be larger, depending on local/regional conditions (Kvambekk, 2012).

Environmental design of water temperature regimes in regulated rivers is challenging and complex, mostly due to various

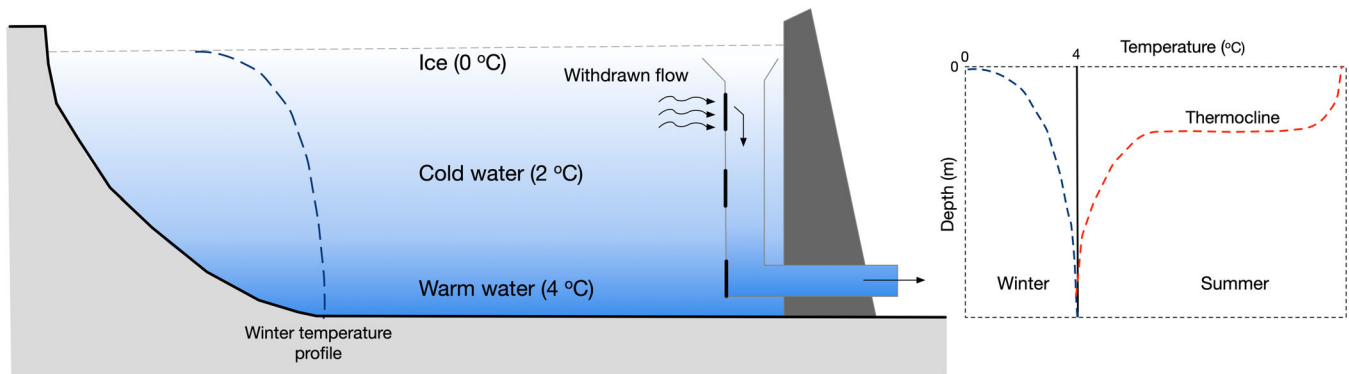


FIGURE 5 Intake control of temperature: multi-level intake structure makes use of the stratification within the reservoir by permitting water with desirable thermal attributes (in this case winter condition, therefore upper layer) to be withdrawn from defined regions within the water column. (Modified after Sherman, 2000) [Color figure can be viewed at wileyonlinelibrary.com]

environmental factors that influence and control water temperature in nature and associated physical-ecological interactions (Table 4).

4.1 | Provide baseline and monitoring data

Baseline data for natural conditions are frequently scarce or lacking. This is a main factor for mitigation, as is just obtaining adequate monitoring data. Recent technological advances have enabled high-resolution GSM/satellite and cellular-based options for monitoring and logging water temperature, light and chemical data in rivers and reservoirs (e.g., Adu-Manu, Tapparello, Heinzelman, Katsriku, & Abdulai, 2017; Myers, 2019; Tauro et al., 2018). These systems should be implemented on regulated rivers, dams/reservoirs, and water transfer schemes, including thermal and hydrological regime monitoring and baselining in environmental flow studies.

Empirical studies are few (Gillespie et al., 2015; Olden & Naiman, 2010; Poff & Zimmerman, 2010), as are lessons learned from implementation of different concrete mitigation measures in regulated systems in northern temperate regions (e.g., Bartholow, Hanna, Saito, Lieberman, & Horn, 2001; Bennet et al., 2011; Gillespie et al., 2015) and much is based on modelling exercises and theory (e.g., Hanna, Saito, Bartholow, & Sandelin, 1999; Bartholow et al., 2001; Sherman, Todd, Koehn, & Ryan, 2007). In particular, there is little empirical data about the long-term biotic responses to environmental variables modified by hydropower flow regulation and water temperature (White et al., 2017). Such studies are necessary to facilitate ecological learning (Table 5) (Roberts, Anderson, & Angermeier, 2016), but unfortunately, too often compromised or omitted altogether from restoration programs (Bash & Ryan, 2002). This may be caused by inadequate funding, deficiencies in the planning process, project timeline, or a mismatch between temporal scales of hydropower flow regulation impacts and monitoring of responses. The lack of pre-project monitoring data, and in many cases, even operational monitoring data and inadequate consideration of appropriate response variables are more serious (Roberts et al., 2016; Rolls, Leigh, & Sheldon, 2012). In addition, the global climate change predictions and the consequences

when combined with thermal regime alterations due to hydropower should be considered (e.g., Benjankar et al., 2018; Cheng, Voisin, Yearsley, & Nijssen, 2020; Palmer et al., 2009). There is also the fundamental question whether one should design mitigation measures to simulate natural conditions, or, if there is a documented potential for it, to “improve” survival/production of economically important, harvestable fish. The precautionary principle suggests the former, although much management has focused on the latter.

Overall, the main mitigation measures depend on reservoir supply and operational strategies, but are basically two: (a) flexible and secondary water release strategies from reservoir to mimic natural water temperature conditions (Figure 5) and (b) methods to increase mixing of surface and bottom water in the reservoir to smoothen water temperature differences with depth (Kvambekk, 2012; Sherman, 2000).

4.2 | Flexible water release

Flexible water release from reservoirs (selective withdrawal) uses a multilevel reservoir intake structure. It is the most effective way of controlling the water temperature of reservoir releases (Figure 5) (Sherman, 2000), providing the opportunity to mimic seasonal variations similar to natural conditions. However, some water temperature differences will remain, depending on release volumes, reservoir stratification, and available water depth intakes. In the hydropower dam on the Alta River (1987), Norway, a secondary upper intake was intended for both summer and winter temperature control releases (Asvall & Kvambekk, 2001). After hydropower regulation, a decline in both Atlantic salmon parr densities (>1+) and adult catch in the upper part of the river (Sautso) was suspected to be caused by the release of warmer water in winter and associated reduced surface ice cover (Ugedal et al., 2008). A trial temperature-flow release program was established (2001–2002) using water from the upper intake to lower the downstream water temperature and to reestablish surface ice cover. This measure theoretically lowered temperatures near to preregulation conditions, but also reduced annual discharge and hydropower production (Asvall & Kvambekk, 2001; Kvambekk, 2012;

Tvede, 2006). Similarly, Olden and Naiman (2010) refer to the Flaming Gorge dam in USA, a somewhat more temperate location, where a multilevel intake was installed in 1978 and increased the downstream summer temperature by 100%, compared to using the original bottom intake. These empirical case studies indicate the mitigation potential with respect to downstream thermal regimes, but more studies are needed to quantify mitigation potential and to consider different hydropower systems (Table 5). Whereas empirical studies appear to be few, a number of modeling studies indicate the feasibility of flexible and/or additional water reservoir intakes for obtaining desired downstream water temperature regimes (Bartholow et al., 2001; Halleraker et al., 2007; Hanna et al., 1999).

The few empirical studies of actual ecological effects on fish and macroinvertebrates of changed temperature releases that exist are mostly from Australia (Miles & West, 2011; Pardo, Campbell, & Brittain, 1998), where amplitudes may be extreme and not comparable to northern temperate regions. In an exceptional time series, 100 years of hydrological and 50 years of aquatic macroinvertebrate assemblage data from the Flaming Gorge dam, Vinson (2001) documented substantial positive results (up to 68% increase in insect taxon richness) after an 100% increase of downstream summer temperatures. Improvements were also observed for the frequency and duration of thermal events, and the timing of extreme temperatures (Olden & Naiman, 2010), although rate and timing of warming remained different from before dam construction (Vinson, 2001). No increase, however, was found in the reach immediately downstream of the dam (0.8 km; Greendale gage). Vinson (2001) suggested this may be explained by the combined effect of three factors: (a) the competitive dominance of insect taxa by amphipods on this reach, (b) low rates of immigration and colonization (from the above reservoir), and (c) low reproductive success of insects due to a few degrees difference in the water temperatures between the regulated river and natural streams in the area. An important general corollary is that not only “traditional” habitat attributes need to be considered, monitored and evaluated in regulated river restoration projects, but biological interactions as well.

Here we contrast two before–after hydropower regulation temperature studies to emphasize that such regulation may generate very different biological impacts, and ecological resilience may depend crucially on timing, and not only on temperature amplitude changes. In the Alta River, North-Norway, hydropower regulation mainly increased fall–winter temperatures (about 0.5–2°C, Figure 3a), increasing degree-days during this egg-incubation period, resulting in earlier hatching in spring. Ecological resilience may be affected by later spawning in fall, and spawning time is known to vary locally (above). Fish growth and production may remain largely unaffected, typically not taking place in this temperature range and season. However, if ice conditions are changed, this may affect fish behavior and survival, which has been a concern (Ugedal et al., 2008). Re-establishing surface ice cover was a main objective of the mitigation efforts (Figure 3a) and could be effected by a modest temperature reduction. In contrast, a similar temperature reduction of 0.5–2°C in Lærdalselva River, West-Norway, occurred in spring–early summer

(Figure 3b). Hydropower regulation will predictably have a major negative effect on fish growth (above) and probably also survival. Bioenergetic modeling (Elliott et al., 1995; Hayes, 2013; Hayes, Stark, & Shearer, 2000) suggests this apparently modest temperature change may generate an annual weight growth reduction of about 25% for a 1 g brown trout (from 3.7 before to 2.8 g after). Unfortunately, because there is little adaptation in fish growth to local temperature regimes, there is little potential for ecological resilience. Thus, unchecked hydropower regulation in northern rivers may typically precipitate a fish production loss via downstream water temperature reduction during the growth season, clearly justifying more focus on thermal regimes and the mitigating potential of flexible water release (Table 5).

4.3 | Water mixing in reservoirs

Water may also be mixed in reservoirs (destratification; Sherman, 2000) to raise water temperature in the hypolimnion in reservoirs with only bottom intakes. One alternative is a bubble plume that creates artificial circulation within the reservoir. Other alternatives include using surface mounted pumps to pump surface water down to the bottom intake, submerged curtains to force surface water to the intake, and curtains that prevent cold, deep water from entering the hydropower intakes (Sherman, 2000; Sherman et al., 2007).

Gray (2016) examined the effects of thermal curtains that directed warmer surface water to the hypolimnial off-take at Burrendong Dam, Australia. The study demonstrated an increase in water temperature of approximately 2°C (mean daily and mean monthly temperature, and diel temperature range) with positive environmental effects (Lugg & Copeland, 2014), as minimum thermal reproductive requirements for local species were met more frequently. Vermeyen (2000) studied the performance of flexible curtains installed in two reservoirs that deliver water to the Sacramento River, USA, to reduce the warm water releases that were exceeding critical levels for Chinook salmon (*Oncorhynchus tshawytscha*) egg incubation and juvenile fish survival. The curtains in Lewiston reservoir contributed to a temperature reduction of 1–2°C, depending on baseload power releases. However, we are not aware of similar studies in northern hydropower regulation systems (Table 5).

5 | CONCLUSIONS AND FUTURE RESEARCH

Water temperature is a controlling factor in ecosystem functioning. For aquatic organisms, seasonal temperature patterns in northern temperate river systems largely define summer as a season for development and growth and winter as the season for tolerance, quiescence, starvation, and survival. Hydropower regulation typically affect thermal regimes primarily in high head systems comprising high elevation reservoirs and transfer tunnels down to lower elevation power plants. High head systems with storage capacity may lead to major

shifts from natural water temperatures. In downstream reaches, water temperatures will typically decrease in summer but increase in winter compared to natural conditions. Hydropeaking systems may generate thermo-peaking exceeding natural daily variations in temperatures and challenge aquatic organisms in terms of life cycle development and fitness. Thus, hydropower-related water temperature changes directly affect aquatic biota. Effects are organism-specific in a variety of ways, in particular for the diverse benthic macroinvertebrate fauna, whereas effects on the species poor northern fish fauna are relatively homogeneous.

A brief overview of considerations reviewed (temperature impacts, responses/consequences, potential mitigating measures), with focus on the life stages of brown trout and Atlantic salmon, is provided in Table 4. Suggested future water temperature and hydropower regulation research and knowledge needs are given in Table 5.

In general, effects of good practice of environmental design and targeted mitigation measures are, unfortunately, not well documented. Much tentative knowledge is based on modelling exercises that need to be empirically validated. Thus, there is a crucial need for more empirical data, especially from long-term studies. The confounding effects of climate change must also be eliminated by the inclusion of non-regulated systems.

ACKNOWLEDGEMENT

This work was funded by Statkraft AS (<https://www.statkraft.com/>) and the University of South-Eastern Norway.

DATA AVAILABILITY STATEMENT

Raw data were generated at Norwegian Water Resources and Energy Directorate—NVE (<https://www.nve.no/english/>). Derived data supporting the findings of this study are available from the corresponding author Jan Heggenes on request.

ORCID

Jan Heggenes  <https://orcid.org/0000-0003-4080-6896>

Knut Alfredsen  <https://orcid.org/0000-0002-4076-8351>

Ana Adeva-Bustos  <https://orcid.org/0000-0001-7655-784X>

REFERENCES

- Adu-Manu, K. S., Tapparello, C., Heinzelman, W., Katsriku, F. A., & Abdulai, J.-D. (2017). Water quality monitoring using wireless sensor networks: Current trends and future research directions. *ACM Transactions on Sensor Networks (TOSN)*, 13, 1–41.
- Alvarez, D., Cano, J. M., & Nicieza, A. G. (2006). Microgeographic variation in metabolic rate and energy storage of brown trout: Countergradient selection or thermal sensitivity? *Evolutionary Ecology*, 20, 345–363.
- Anderson, K., Swanson, P., Pankhurst, N., King, H., & Elizur, A. (2012). Effect of thermal challenge on plasma gonadotropin levels and ovarian steroidogenesis in female maiden and repeat spawning Tasmanian Atlantic salmon (*Salmo salar*). *Aquaculture*, 334, 205–212.
- Angilletta, M. J., Jr., Steury, T. D., & Sears, M. W. (2004). Temperature, growth rate, and body size in Ectotherms: Fitting pieces of a life-history Puzzle1. *Integrative and Comparative Biology*, 44, 498–509.
- Angilletta, M. J., Niewiarowski, P. H., & Navas, C. A. (2002). The evolution of thermal physiology in ectotherms. *Journal of Thermal Biology*, 27, 249–268.
- Anttila, K., Dhillon, R. S., Boulding, E. G., Farrell, A. P., Glebe, B. D., Elliott, J. A. K., ... Schulte, P. M. (2013). Variation in temperature tolerance among families of Atlantic salmon (*Salmo salar*) is associated with hypoxia tolerance, ventricle size and myoglobin level. *Journal of Experimental Biology*, 216, 1183–1190.
- Archer, D. (2008). *The influence of river regulation at Kielder water on the thermal regime of the river North Tyne*. BHS 10th National Hydrology Symposium, pp. 35–41. Retrieved from https://www.researchgate.net/publication/273137677_The_influence_of_river_regulation_at_Kielder_Water_on_the_thermal_regime_of_the_River_North_Tyne
- Asvall, R., & Kvambekk, Å. (2001). Ny strategi for tapping av Altamagasinet om vinteren. Endring av vanntemperatur og isregimet fra utløpet av kraftstasjonen i Savco ved utvidet bruk av øvre inntak. NVE Oppdragsrapport. Report number 10-2001. Retrieved from http://publikasjoner.nve.no/oppdragsrapport/2001/oppdragsrapport2001_10.pdf
- Asvall, R. P. (1977). *Vanntemperatur og isforhold i våre vassdrag*. Generelt om virkningen av vassdragsreguleringer i berørte vassdrag og tilstøtende fjorder. Rapport Vassdragsdirektoratet. Vassdragsdirektoratet, Oslo, Norway.
- Asvall, R. P. (2008). *Altautbyggingen-Vanntemperatur og isforhold om vinteren (2007-2008)*. NVE Oppdragsrapport A. Norges Vassdrags og Energidirektorat, Norges Vassdrags og Energidirektorat Oslo. p. 28. Retrieved from http://publikasjoner.nve.no/oppdragsrapportA/2008/oppdragsrapportA2008_13.pdf
- Austin, H., Bradley, D., Steward-Rousson, I., & Milner, N. (2015). *Literature review of the influence of large impoundments on downstream temperature, water quality and ecology, with reference to the water framework directive*. APEM scientific report. Scottish Environmental Protection Agency, Stirling, Scotland. p. 84.
- Ayllon, D., Nicola, G. G., Elvira, B., Parra, I., & Almodovar, A. (2013). Thermal carrying capacity for a thermally-sensitive species at the warmest edge of its range. *PLoS One*, 8, 11.
- Baerum, K. M., Vollestad, L. A., Kiffney, P., Remy, A., & Haugen, T. O. (2016). Population-level variation in juvenile brown trout growth from different climatic regions of Norway to an experimental thermal gradient. *Environmental Biology of Fishes*, 99, 1009–1018.
- Bakken, T. H., King, T., & Alfredsen, K. (2016). Simulation of river water temperatures during various hydro-peaking regimes. *Journal of Applied Water Engineering and Research*, 4, 31–43.
- Bale, J. S., & Hayward, S. A. L. (2010). Insect overwintering in a changing climate. *Journal of Experimental Biology*, 213, 980–994.
- 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.
- Barneche, D. R., & Allen, A. P. (2018). The energetics of fish growth and how it constrains food-web trophic structure. *Ecology Letters*, 21, 836–844.
- Bartholow, J., Hanna, R., Saito, L., Lieberman, D., & Horn, M. (2001). Simulated Limnological effects of the Shasta Lake temperature control device. *Environmental Management*, 27, 609–626.
- Bash, J. S., & Ryan, C. M. (2002). Stream restoration and enhancement projects: Is anyone monitoring? *Environmental Management*, 29, 877–885.
- Beach, M. H. (1984). Fish pass design-criteria for the design and approval of fish passes and other structures to facilitate the passage of migratory fish in rivers Fisheries Reserach Technical Report. Ministry of Agriculture, Fisheries and Food, Lowestoft, England. p. 48. Retrieved from <http://aquaticcommons.org/8065/>
- Beamish, F. W. (1979). 2. Swimming capacity. In W. S. Hoar & D. J. Randall (Eds.), *Locomotion* (pp. 101–187). New York: Academic Press Inc.
- Beitinger, T. L., Bennett, W. A., & McCauley, R. W. (2000). Temperature tolerances of north American freshwater fishes exposed to dynamic changes in temperature. *Environmental Biology of Fishes*, 58, 237–275.

- Benjankar, R., Tonina, D., McKean, J. A., Sohrabi, M. M., Chen, Q., & Videgar, D. (2018). Dam operations may improve aquatic habitat and offset negative effects of climate change. *Journal of Environmental Management*, 213, 126–134.
- Bennet, W., Rybel, V., Jenkins, M., Donohue, K., Riker, R., & Sticka, D. (2011). Retrofitting a deep water plant intake to improve fish passage. *HydroReview*, 30, 38–46.
- Benson, N. G. (1955). Observations on anchor ice in a Michigan trout stream. *Ecology*, 36, 529–530.
- Berg, O. K., Finstad, A. G., Solem, O., Ugedal, O., Forseth, T., Niemela, E., ... Naesje, T. F. (2009). Pre-winter lipid stores in young-of-year Atlantic salmon along a north-south gradient. *Journal of Fish Biology*, 74, 1383–1393.
- Berg, O. K., Rod, G., Solem, O., & Finstad, A. G. (2011). Pre-winter lipid stores in brown trout *Salmo trutta* along altitudinal and latitudinal gradients. *Journal of Fish Biology*, 79, 1156–1166.
- Bradshaw, W. E., Zani, P. A., & Holzapfel, C. M. (2004). Adaptation to temperate climates. *Evolution*, 58, 1748–1762.
- Breau, C., Cunjak, R. A., & Peake, S. J. (2011). Behaviour during elevated water temperatures: Can physiology explain movement of juvenile Atlantic salmon to cool water? *Journal of Animal Ecology*, 80, 844–853.
- Bret, V., Bergerot, B., Capra, H., Gouraud, V., & Lamouroux, N. (2016). Influence of discharge, hydraulics, water temperature, and dispersal on density synchrony in brown trout populations (*Salmo trutta*). *Canadian Journal of Fisheries and Aquatic Sciences*, 73, 319–329.
- Brinck, P. (1949). Studies on Swedish stoneflies (Plecoptera). *Opuscula Entomologica*, 11, 1–250.
- Brittain, J. E. (1982). Biology of mayflies. *Annual Review of Entomology*, 27, 119–147.
- Brittain, J. E. (1983). The influence of temperature on nymphal growth-rates in mountain stoneflies (Plecoptera). *Ecology*, 64, 440–446.
- Brittain, J. E. (1990). Life history strategies in Ephemeroptera and Plecoptera. In I. C. Campbell (Ed.), *Mayflies and stoneflies* (pp. 1–12). Dordrecht: Kluwer Press.
- Brittain, J. E. (1991). Life history characteristics as a determinant of the response of mayflies and stoneflies to man-made environmental disturbance. In J. Alba-Tercedor (Ed.), *Overview and strategies of Ephemeroptera and Plecoptera* (pp. 539–545). Gainesville, Florida: Sandhill Crane Press.
- Brittain, J. E., & Eikeland, T. J. (1988). Invertebrate drift—a review. *Hydrobiologia*, 166, 77–93.
- Brittain, J. E., & Saltveit, S. J. (1989). A review of the effect of river regulation on mayflies (Ephemeroptera). *Regulated Rivers: Research & Management*, 3, 191–204.
- Brown, C. J. D., Clothier, W. D., & Alvord, W. (1953). *Observations on ice conditions and bottom organisms in the West Gallatin River*. Montana: Montana Academy of Sciences. 13, 21–27.
- Brown, L. E., Hannah, D. M., & Milner, A. M. (2006). Thermal variability and stream flow permanency in an alpine river system. *River Research and Applications*, 22, 493–501.
- Bruno, M. C., Maiolini, B., Carolli, M., & Silveri, L. (2009). Impact of hydropeaking on hyporheic invertebrates in an alpine stream (Trentino, Italy). *Annales De Limnologie-International Journal of Limnology*, 45, 157–170.
- Bruno, M. C., Siviglia, A., Carolli, M., & Maiolini, B. (2013). Multiple drift responses of benthic invertebrates to interacting hydropeaking and thermopeaking waves. *Ecohydrology*, 6, 511–522.
- Budy, P., Thiede, G. P., Lobon-Cervia, J., Fernandez, G. G., McHugh, P., McIntosh, A., ... Jellyman, P. (2013). Limitation and facilitation of one of the world's most invasive fish: An intercontinental comparison. *Ecology*, 94, 356–367.
- Butler, R. L., & Hawthorne, V. M. (1979). Anchor ice, its formation and effects on aquatic life. *Science in Agriculture*, 26(2), 2.
- Byrne, C. J., Poole, R., Dillane, M., Rogan, G., & Whelan, K. F. (2004). Temporal and environmental influences on the variation in sea trout (*Salmo trutta* L.) smolt migration in the Burrishoole system in the west of Ireland from 1971 to 2000. *Fisheries Research*, 66, 85–94.
- Cadbury, S., Hannah, D., Milner, A., Pearson, C., & Brown, L. (2008). Stream temperature dynamics within a New Zealand glacierized river basin. *River Research and Applications*, 24, 68–89.
- Caissie, D. (2006). The thermal regime of rivers: A review. *Freshwater Biology*, 51, 1389–1406.
- Casas-Mulet, R., Alfredsen, K., Brabrand, A., & Saltveit, S. J. (2015). Survival of eggs of Atlantic salmon (*Salmo salar*) in a drawdown zone of a regulated river influenced by groundwater. *Hydrobiologia*, 743, 269–284.
- Casas-Mulet, R., Alfredsen, K., Brabrand, A., & Saltveit, S. J. (2016). Hydro-power operations in groundwater-influenced rivers: Implications for Atlantic salmon, *Salmo salar*, early life stage development and survival. *Fisheries Management and Ecology*, 23, 144–151.
- Casas-Mulet, R., Alfredsen, K., Hamududu, B., & Timalina, N. P. (2015). The effects of hydropeaking on hyporheic interactions based on field experiments. *Hydrological Processes*, 29, 1370–1384.
- Casas-Mulet, R., Saltveit, S. J., & Alfredsen, K. (2015). The survival of Atlantic salmon (*Salmo salar*) eggs during dewatering in a river subjected to hydropeaking. *River Research and Applications*, 31, 433–446.
- Casas-Mulet, R., Saltveit, S. J., & Alfredsen, K. T. (2016). Hydrological and thermal effects of hydropeaking on early life stages of salmonids: A modelling approach for implementing mitigation strategies. *Science of the Total Environment*, 573, 1660–1672.
- Catrinu-Renström, M., & Knudsen, J. (2011). *Perspectives on hydropower's role to balance non-regulated renewable power production in northern Europe*. SINTEF Report. SINTEF, Trondheim. p. 126. Retrieved from <http://hdl.handle.net/11250/2448210>
- Cereghino, R., Cugny, P., & Lavandier, P. (2002). Influence of intermittent hydropeaking on the longitudinal zonation patterns of benthic invertebrates in a mountain stream. *International Review of Hydrobiology*, 87, 47–60.
- Cheng, Y., Voisin, N., Yearsley, J. R., & Nijssen, B. (2020). Reservoirs Modify River thermal regime sensitivity to climate change: A case study in the southeastern United States. *Water Resources Research*, 56, e2019WR025784.
- Chezik, K. A., Lester, N. P., & Venturelli, P. A. (2014). Fish growth and degree-days I: Selecting a base temperature for a within-population study. *Canadian Journal of Fisheries and Aquatic Sciences*, 71, 47–55.
- Clarke, A., & Portner, H. O. (2010). Temperature, metabolic power and the evolution of endothermy. *Biological Reviews*, 85, 703–727.
- Clifford, H. F. (1972). A years' study of the drifting organisms in a brown-water stream of Alberta, Canada. *Canadian Journal of Zoology*, 50, 975–983.
- Colbo, M. (1979). Distribution of winter-developing Simuliidae (Diptera), in eastern Newfoundland. *Canadian Journal of Zoology*, 57, 2143–2152.
- Constantz, J. (1998). Interaction between stream temperature, streamflow, and groundwater exchanges in alpine streams. *Water Resources Research*, 34, 1609–1615.
- Coulson, S. J., Convey, P., Aakra, K., Aarvik, L., Avila-Jimenez, M. L., Babenko, A., ... Zmudzynska-Skarbek, K. (2014). The terrestrial and freshwater invertebrate biodiversity of the archipelagoes of the Barents Sea, Svalbard, Franz Josef Land and Novaya Zemlya. *Soil Biology & Biochemistry*, 68, 440–470.
- Crespel, A., Bernatchez, L., Garant, D., & Audet, C. (2013). Genetically based population divergence in overwintering energy mobilization in brook charr (*Salvelinus fontinalis*). *Genetica*, 141, 51–64.
- Crozier, L. G., & Hutchings, J. A. (2014). Plastic and evolutionary responses to climate change in fish. *Evolutionary Applications*, 7, 68–87.
- Cunjak, R. A., Linnansaari, T., & Caissie, D. (2013). The complex interaction of ecology and hydrology in a small catchment: A salmon's perspective. *Hydrological Processes*, 27, 741–749.

- Dallas, H., & Ross-Gillespie, V. (2015). Sublethal effects of temperature on freshwater organisms, with special reference to aquatic insects. *Water SA*, 41, 712–726.
- Danks, H. V. (2008). Aquatic insets adaptations to winter cold and ice. In J. Lancaster & R. A. Briers (Eds.), *Aquatic insects: Challenges to populations: Proceedings of the Royal Entomological Society's 24th Symposium* (pp. 1–19). Wallingford, Oxfordshire, England: CAB International.
- Dekar, M. P., Magoulick, D. D., & Huxel, G. R. (2009). Shifts in the trophic base of intermittent stream food webs. *Hydrobiologia*, 635, 263–277.
- Dell, A. I., Pawar, S., & Savage, V. M. (2011). Systematic variation in the temperature dependence of physiological and ecological traits. *Proceedings of the National Academy of Sciences of the United States of America*, 108, 10591–10596.
- Dickson, N. E., Carrivick, J. L., & Brown, L. E. (2012). Flow regulation alters alpine river thermal regimes. *Journal of Hydrology*, 464, 505–516.
- Dugdale, S. J., Malcolm, I. A., Kantola, K., & Hannah, D. M. (2018). Stream temperature under contrasting riparian forest cover: Understanding thermal dynamics and heat exchange processes. *Science of the Total Environment*, 610, 1375–1389.
- Einum, S., Finstad, A. G., Robertsen, G., Nislow, K. H., McKelvey, S., & Armstrong, J. D. (2012). Natal movement in juvenile Atlantic salmon: A body size-dependent strategy? *Population Ecology*, 54, 285–294.
- Einum, S., & Fleming, I. A. (2000). Selection against late emergence and small offspring in Atlantic salmon (*Salmo salar*). *Evolution*, 54, 628–639.
- Einum, S., Robertsen, G., Nislow, K. H., McKelvey, S., & Armstrong, J. D. (2011). The spatial scale of density-dependent growth and implications for dispersal from nests in juvenile Atlantic salmon. *Oecologia*, 165, 959–969.
- Elliott, J. A. (1981). Some aspects of thermal stress on freshwater teleosts. In A. D. Pickering (Ed.), *Stress and fish* (pp. 209–246). London: Academic Press.
- Elliott, J. M. (1985). Population regulation for different life-stages of migratory trout *salmo-trutta* in a lake district stream, 1966–83. *Journal of Animal Ecology*, 54, 617–638.
- Elliott, J. M. (1989). The natural regulation of numbers and growth in contrasting populations of brown trout, *salmo-trutta*, in 2 lake district streams. *Freshwater Biology*, 21, 7–19.
- Elliott, J. M. (1994). *Quantitative ecology and the Brown trout*. Oxford: Oxford University Press.
- Elliott, J. M. (2009). Validation and implications of a growth model for brown trout, *Salmo trutta*, using long-term data from a small stream in north-West England. *Freshwater Biology*, 54, 2263–2275.
- Elliott, J. M. (2011). A comparative study of the relationship between light intensity and feeding ability in brown trout (*Salmo trutta*) and Arctic charr (*Salvelinus alpinus*). *Freshwater Biology*, 56, 1962–1972.
- Elliott, J. M. (2015). Density-dependent and density-independent growth in a population of juvenile sea-trout, *Salmo trutta*, assessed using long-term data from a small stream in Northwest England. *Freshwater Biology*, 60, 336–346.
- Elliott, J. M., & 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.
- Elliott, J. M., & Hurley, M. A. (1997). A functional model for maximum growth of Atlantic Salmon parr, *Salmo salar*, from two populations in Northwest England. *Functional Ecology*, 11, 592–603.
- Elliott, J. M., & Hurley, M. A. (1998a). Population regulation in adult, but not juvenile, resident trout (*Salmo trutta*) in a Lake District stream. *Journal of Animal Ecology*, 67, 280–286.
- Elliott, J. M., & Hurley, M. A. (1998b). Predicting fluctuations in the size of newly emerged sea-trout fry in a Lake District stream. *Journal of Fish Biology*, 53, 1120–1133.
- Elliott, J. M., Hurley, M. A., & Fryer, R. J. (1995). A new, improved growth-model for brown trout. *Salmo trutta*. *Functional Ecology*, 9, 290–298.
- Ellis, L. E., & Jones, N. E. (2013). Longitudinal trends in regulated rivers: A review and synthesis within the context of the serial discontinuity concept. *Environmental Reviews*, 21, 136–148.
- Embrey, G. C. (1934). Relation of temperature to the incubation periods of eggs of four species of trout. *Transactions of the American Fisheries Society*, 64, 281–292.
- Ettema, R., Kirkil, G., & Daly, S. (2009). Frazil ice concerns for channels, pump-lines, penstocks, siphons, and tunnels in mountainous regions. *Cold Regions Science and Technology*, 55, 202–211.
- Ferreira, V., & Canhoto, C. (2014). Effect of experimental and seasonal warming on litter decomposition in a temperate stream. *Aquatic Sciences*, 76, 155–163.
- Finni, G. R., & Chandler, L. (1979). The microdistribution of *Allocapnia naiads* Plecoptera: Capniidae. *Journal of the Kansas Entomological Society*, 52, 93–102.
- Finstad, A., Berg, O. K., Forseth, T., Ugedal, O., & Naesje, T. F. (2010). Adaptive winter survival strategies: Defended energy levels in juvenile Atlantic salmon along a latitudinal gradient. *Proceedings of the Royal Society B-Biological Sciences*, 277, 1113–1120.
- Finstad, A. G., & Forseth, T. (2006). Adaptation to ice-cover conditions in Atlantic salmon, *Salmo salar* L. *Evolutionary Ecology Research*, 8, 1249–1262.
- Finstad, A. G., Forseth, T., Faenstad, T. F., & Ugedal, O. (2004). The importance of ice cover for energy turnover in juvenile Atlantic salmon. *Journal of Animal Ecology*, 73, 959–966.
- Finstad, A. G., & Jonsson, B. (2012). Effect of incubation temperature on growth performance in Atlantic salmon. *Marine Ecology Progress Series*, 454, 75–82.
- Finstad, A. G., Naesje, T. F., & Forseth, T. (2004). Seasonal variation in the thermal performance of juvenile Atlantic salmon (*Salmo salar*). *Freshwater Biology*, 49, 1459–1467.
- Forseth, T., Hurley, M. A., Jensen, A. J., & Elliott, J. M. (2001). Functional models for growth and food consumption of Atlantic salmon parr, *Salmo salar*, from a Norwegian river. *Freshwater Biology*, 46, 173–186.
- Forseth, T., & Jonsson, B. (1994). The growth and food ration of piscivorous brown trout (*Salmo trutta*). *Functional Ecology*, 8, 171–177.
- Forseth, T., Larsson, S., Jensen, A. J., Jonsson, B., Naslund, I., & Berglund, I. (2009). Thermal growth performance of juvenile brown trout *Salmo trutta*: No support for thermal adaptation hypotheses. *Journal of Fish Biology*, 74, 133–149.
- Forseth, T., Letcher, B. H., & Johansen, M. (2010). The Behavioural flexibility of Salmon growth. In *Atlantic salmon ecology* (pp. 145–169). Chichester: Wiley-Blackwell. <https://doi.org/10.1002/9781444327755>.
- Frisbie, M. P., & Lee, R. E. (1997). Inoculative freezing and the problem of winter survival for freshwater macroinvertebrates. *Journal of the North American Benthological Society*, 16, 635–650.
- Fry, F. E. J. (1971). The effect of environmental factors on the physiology of fish. In W. S. Hoar & D. J. Randall (Eds.), *Fish physiology* (pp. 1–98). New York, NY: Academic Press.
- Gebre, S., Alfredsen, K., Lia, L., Stickler, M., & Tesaker, E. (2013). Ice effects on hydropower systems—a review. *Journal of Cold Regions Engineering*, 27, 196–222.
- Geris, J., Tetzlaff, D., Seibert, J., Vis, M., & Soulsby, C. (2015). Conceptual modelling to assess hydrological impacts and evaluate environmental flow scenarios in montane river systems regulated for hydropower. *River Research and Applications*, 31, 1066–1081.
- Gibbins, C., Shellberg, J., Moir, H. J., & Soulsby, C. (2008). Hydrological influences on adult salmonid migration, spawning and embryo survival. In D. Sear & P. DeVries (Eds.), *Salmon spawning habitat in rivers: Physical controls, biological responses and approaches* (pp. 195–224). Bethesda, Maryland: American Fisheries Society.

- Gibson, R. J., & Myers, R. A. (1988). Influence of seasonal river discharge on survival of juvenile Atlantic salmon, *salmo-salar*. *Canadian Journal of Fisheries and Aquatic Sciences*, 45, 344–348.
- Gillespie, B. R., Desmet, S., Kay, P., Tillotson, M. R., & Brown, L. E. (2015). A critical analysis of regulated river ecosystem responses to managed environmental flows from reservoirs. *Freshwater Biology*, 60, 410–425.
- Graham, C. T., & Harrod, C. (2009). Implications of climate change for the fishes of the British Isles. *Journal of Fish Biology*, 74, 1143–1205.
- Gray, R. L. (2016). *Effectiveness of cold water pollution mitigation at Burrendong Dam using an innovative thermal curtain*. UTS Digital Theses Collection. Retrieved from <http://hdl.handle.net/10453/44199>
- 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.
- Gunderson, A. R., & Stillman, J. H. (2015). Plasticity in thermal tolerance has limited potential to buffer ectotherms from global warming. *Proceedings of the Royal Society B: Biological Sciences*, 282, 20150401.
- Gunnes, K. (1979). Survival and development of Atlantic salmon eggs and fry at 3 different temperatures. *Aquaculture*, 16, 211–218.
- Haapala, A., & Muotka, T. (1998). Seasonal dynamics of detritus and associated macroinvertebrates in a channelized boreal stream. *Archiv Fur Hydrobiologie*, 142, 171–189.
- Haapala, A., Muotka, T., & Markkola, A. (2001). Breakdown and macroinvertebrate and fungal colonization of alder, birch, and willow leaves in a boreal forest stream. *Journal of the North American Benthological Society*, 20, 395–407.
- Hågvar, S., & Østbye, E. (1973). Notes on some Winter-Active Chironomidae. *Norsk entomologisk tidsskrift*, 20, 253–257.
- Halleraker, J. H., Sundt, H., Alfredsen, K. T., & Dangelmaier, G. (2007). Application of multiscale environmental flow methodologies as tools for optimized management of a Norwegian regulated national salmon watercourse. *River Research and Applications*, 23, 493–510.
- Hamblin, P., & McAdam, S. (2003). Impoundment effects on the thermal regimes of Kootenay Lake, the Arrow Lakes reservoir and upper Columbia River. *Hydrobiologia*, 504, 3–19.
- Hanna, R., Saito, L., Bartholow, J., & Sandelin, J. (1999). Results of simulated temperature control device operations on in-reservoir and discharge water temperatures using CE-QUAL-W2. *Lake and Reservoir Management*, 15, 87–102.
- Hansen, L. P., & Jonsson, B. (1985). Downstream migration of hatchery-reared smolts of Atlantic salmon (*Salmo salar* L) in the river Imsa, Norway. *Aquaculture*, 45, 237–248.
- Harper, P., & Hynes, H. (1970). Diapause in the nymphs of Canadian winter stoneflies. *Ecology*, 51, 925–927.
- Hartman, K. J., & Porto, M. A. (2014). Thermal performance of three rainbow trout strains at above-optimal temperatures. *Transactions of the American Fisheries Society*, 143, 1445–1454.
- Haxton, T. J., & Findlay, C. S. (2008). Meta-analysis of the impacts of water management on aquatic communities. *Canadian Journal of Fisheries and Aquatic Sciences*, 65, 437–447.
- Hayes, J. W. (2013). *Brown trout growth models: User guide version 2.1*. Cawthron Report No. 571A. Cawthron Institute, Cawthron Institute, Nelson, New Zealand. p. 46.
- Hayes, J. W., Stark, J. D., & Shearer, K. A. (2000). Development and test of a whole-lifetime foraging and bioenergetics growth model for drift-feeding brown trout. *Transactions of the American Fisheries Society*, 129, 315–332.
- Hedger, R. D., Sundt-Hansen, L. E., Forseth, T., Ugedal, O., Diserud, O. H., Kvambekk, A. S., & Finstad, A. G. (2013). Predicting climate change effects on subarctic-Arctic populations of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, 70, 159–168.
- Heggberget, T. G., & Wallace, J. C. (1984). Incubation of the eggs of Atlantic salmon, *Salmo salar*, at low-temperatures. *Canadian Journal of Fisheries and Aquatic Sciences*, 41, 389–391.
- Hegggenes, J., Alfredsen, K., Brittain, J. E., Bustos, A. A., Huusko, A., & Stickler, M. (2017). *Stay cool: Temperature changes and biological responses in hydropower-regulated northern stream systems: HSN Skrift* (p. 95). Bø i Telemark: University College of Southeast Norway. <http://hdl.handle.net/11250/2477901>.
- Hegggenes, J., Alfredsen, K., Bustos, A. A., Huusko, A., & Stickler, M. (2017). Be cool: A review of hydro-physical changes and fish responses in winter in hydropower-regulated northern streams. *Environmental Biology of Fishes*, 101, 1–21.
- Heino, J., Erkinaro, J., Huusko, A., & Luoto, M. (2016). Climate change effects on freshwater fishes, conservation and management. In G. P. Closs, M. Krkosek, & J. D. Olden (Eds.), *Conservation of freshwater fishes* (pp. 76–106). Cambridge: Cambridge University Press, UK.
- Hildebrand, S. G. (1974). Relation of drift to benthos density and food level in an artificial stream. *Limnology and Oceanography*, 19, 951–957.
- Hoffsten, P. O. (2003). Effects of an extraordinarily harsh winter on macroinvertebrates and fish in boreal streams. *Archiv Fur Hydrobiologie*, 157, 505–523.
- Huryn, A. D., & Wallace, J. B. (2000). Life history and production of stream insects. *Annual Review of Entomology*, 45, 83–110.
- Hutchison, V. H., & Maness, J. D. (1979). The role of behavior in temperature acclimation and tolerance in ectotherms. *American Zoologist*, 19, 367–384.
- Huusko, A., Maki-Petays, A., Stickler, M., & Mykra, H. (2011). Fish can shrink under harsh living conditions. *Functional Ecology*, 25, 628–633.
- Hynes, H. B. N. (1970). *The ecology of running waters*. Toronto, Canada: University of Toronto Press. <https://doi.org/10.4319/lo.1971.16.3.0593>.
- Irons, J. G., Miller, L. K., & Oswood, M. W. (1993). Ecological adaptations of aquatic macroinvertebrates to overwintering in interior Alaska (USA) subarctic streams. *Canadian Journal of Zoology*, 71, 98–108.
- Jackson, H., Gibbins, C., & Soulsby, C. (2007). Role of discharge and temperature variation in determining invertebrate community structure in a regulated river. *River Research and Applications*, 23, 651–669.
- Jensen, A. J. (1990). Growth of young migratory brown trout *Salmo trutta* correlated with water temperature in Norwegian Rivers. *Journal of Animal Ecology*, 59, 603–614.
- Jensen, A. J., Forseth, T., & Johnsen, B. O. (2000). Latitudinal variation in growth of young brown trout *Salmo trutta*. *Journal of Animal Ecology*, 69, 1010–1020.
- Jensen, A. J., & Johnsen, B. O. (1999). The functional relationship between peak spring floods and survival and growth of juvenile Atlantic Salmon (*Salmo salar*) and Brown trout (*Salmo trutta*). *Functional Ecology*, 13, 778–785.
- Jensen, A. J., Johnsen, B. O., & Heggberget, T. G. (1991). Initial feeding time of Atlantic Salmon, *Salmo salar*, alevins compared to river flow and water temperature in norwegian streams. *Environmental Biology of Fishes*, 30, 379–385.
- Jensen, A. J., Johnsen, B. O., & Saksgard, 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.
- Jensen, L. F., Hansen, M. M., Pertoldi, C., Holdensgaard, G., Mensberg, K. L. D., & Loeschcke, V. (2008). Local adaptation in brown trout early life-history traits: Implications for climate change adaptability. *Proceedings of the Royal Society B-Biological Sciences*, 275, 2859–2868.
- Jonsson, B., Forseth, T., Jensen, A. J., & Naesje, T. F. (2001). Thermal performance of juvenile Atlantic Salmon, *Salmo salar* L. *Functional Ecology*, 15, 701–711.
- 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.

- Jonsson, B., & Labée-Lund, J. H. (1993). Latitudinal clines in life-history variables of anadromous brown trout in Europe. *Journal of Fish Biology*, 43, 1–16.
- Jonsson, B., & Ruud-Hansen, J. (1985). Water temperature as the primary influence on timing of seaward migrations of Atlantic salmon (*Salmo salar*) smolts. *Canadian Journal of Fisheries and Aquatic Sciences*, 42, 593–595.
- Jonsson, N., Jonsson, B., & Hansen, L. P. (1998). Long-term study of the ecology of wild Atlantic salmon smolts in a small Norwegian river. *Journal of Fish Biology*, 52, 638–650.
- Juanes, F., Gephard, S., & Beland, K. (2004). Long-term changes in migration timing of adult Atlantic salmon (*Salmo salar*) at the southern edge of the species distribution. *Canadian Journal of Fisheries and Aquatic Sciences*, 61, 2392–2400.
- 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.
- Kane, T. R. (1988). Relationship of temperature and time of initial feeding of Atlantic salmon. *Progressive Fish-Culturist*, 50, 93–97.
- 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.
- Kvambeek, A. S. (2004). *Vanntemperaturer i Suldalslågen. Simulering av uregulert tilstand i 1931-2002 og ulike skisseforslag til nytt vannføringsregime*. NVE Miljørapport, Norges Vassdrags og Energidirektorat, Norges Vassdrags og Energidirektorat Oslo. p. 50. Retrieved from https://www.statkraft.com/globalassets/old-contains-the-old-folder-structure/documents/no/31-vanntemperaturer-i-suldalslagen.-simulering-av-uregulert-tilstand-i-1931-2002-og-ulike-skisseforslag-til-nytt-vannforingsregime_tcm10-4190.pdfhttps://www.statkraft.com/globalassets/old-contains-the-old-folder-structure/documents/no/31-vanntemperaturer-i-suldalslagen.-simulering-av-uregulert-tilstand-i-1931-2002-og-ulike-skisseforslag-til-nytt-vannforingsregime_tcm10-4190.pdf
- Kvambeek, Å. S. (2012). *Vanntemperatur i kraftverksmagasiner-Hvilke temperaturforskjeller kan oppnås ved bruk av flere inntaksdyp? Rapport Miljøbasert Vannføring, Norges Vassdrags og Energidirektorat, Norges Vassdrags og Energidirektorat Oslo*. p. 33. Retrieved from https://publikasjoner.nve.no/rapport_miljoebasert_vannfoering/2012/miljoebasert2012_07.pdf
- Larsson, S., & Berglund, I. (2006). Thermal performance of juvenile Atlantic salmon (*Salmo salar* L.) of Baltic Sea origin. *Journal of Thermal Biology*, 31, 243–246.
- Lencioni, V. (2004). Survival strategies of freshwater insects in cold environments. *Journal of Limnology*, 63, 45–55.
- Letcher, B. H., Dubreuil, T., O'Donnell, M. J., Obedzinski, M., Griswold, K., & Nislow, K. H. (2004). Long-term consequences of variation in timing and manner of fry introduction on juvenile Atlantic salmon (*Salmo salar*) growth, survival, and life-history expression. *Canadian Journal of Fisheries and Aquatic Sciences*, 61, 2288–2301.
- Lien, L. (1978). The energy budget of the Brown trout population of Øvre Heimdalsvatn. *Holarctic Ecology*, 1, 279–300.
- Lillehammer, A. (1987). Diapause and quiescence in eggs of Systellognatha stonefly species (Plecoptera) occurring in alpine areas of Norway. *Annales de Limnologie - International Journal of Limnology*, 23, 179–184.
- Lillehammer, A., Brittain, J. E., Saltveit, S. J., & Nielsen, P. S. (1989). Egg development, nymphal growth and life-cycle strategies in Plecoptera. *Holarctic Ecology*, 12, 173–186.
- Linnansaari, T., Alfredsen, K., Stickler, M., Arnekleiv, J. V., Harby, A., & Cunjak, R. A. (2009). Does ice matter? Site fidelity and movements by Atlantic salmon (*Salmo salar* L.) parr during winter in a substrate enhanced river reach. *River Research and Applications*, 25, 773–787.
- Lobon-Cervia, J. (2014). Recruitment and survival rate variability in fish populations: Density-dependent regulation or further evidence of environmental determinants? *Canadian Journal of Fisheries and Aquatic Sciences*, 71, 290–300.
- Lobon-Cervia, J., & Mortensen, E. (2005). Population size in stream-living juveniles of lake-migratory brown trout *Salmo trutta* L.: The importance of stream discharge and temperature. *Ecology of Freshwater Fish*, 14, 394–401.
- Lobon-Cervia, J., & Rincon, P. A. (1998). Field assessment of the influence of temperature on growth rate in a brown trout population. *Transactions of the American Fisheries Society*, 127, 718–728.
- Logez, M., & Pont, D. (2011). Variation of brown trout *Salmo trutta* young-of-the-year growth along environmental gradients in Europe. *Journal of Fish Biology*, 78, 1269–1276.
- Lugg, A., & Copeland, C. (2014). Review of cold water pollution in the Murray–Darling basin and the impacts on fish communities. *Ecological Management & Restoration*, 15, 71–79.
- Magnuson, J. J., Crowder, L. B., & Medvick, P. A. (1979). Temperature as an ecological resource. *American Zoologist*, 19, 331–343.
- Malcolm, I. A., Gibbins, C. N., Soulsby, C., Tetzlaff, D., & Moir, H. J. (2012). The influence of hydrology and hydraulics on salmonids between spawning and emergence: Implications for the management of flows in regulated rivers. *Fisheries Management and Ecology*, 19, 464–474.
- Martin, M. D., Brown, R. S., Barton, D. R., & Power, G. (2001). Abundance of stream invertebrates in winter: Seasonal changes and effects of river ice. *Canadian Field-Naturalist*, 115, 68–74.
- 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.
- Meier, K., Hansen, M. M., Normandeau, E., Mensberg, K. L. D., Frydenberg, J., Larsen, P. F., ... Bernatchez, L. (2014). Local adaptation at the Transcriptome level in Brown trout: Evidence from early life history temperature genomic reaction norms. *PLoS One*, 9, e85171.
- Metcalfe, N. B., Fraser, N. H. C., & Burns, M. D. (1999). Food availability and the nocturnal vs. diurnal foraging trade-off in juvenile salmon. *Journal of Animal Ecology*, 68, 371–381.
- Metcalfe, N. B., & Thorpe, J. E. (1990). Determinants of geographical variation in the age of seaward migrating salmon, *Salmo salar*. *Journal of Animal Ecology*, 59, 135–145.
- Miles, N. G., & West, R. J. (2011). The use of an aeration system to prevent thermal stratification of a freshwater impoundment and its effect on downstream fish assemblages. *Journal of Fish Biology*, 78, 945–952.
- Miller, S. W., & Judson, S. (2014). Responses of macroinvertebrate drift, benthic assemblages, and trout foraging to hydropeaking. *Canadian Journal of Fisheries and Aquatic Sciences*, 71, 675–687.
- Milner, N. J., Elliott, J. M., Armstrong, J. D., Gardiner, R., Welton, J. S., & Ladle, M. (2003). The natural control of salmon and trout populations in streams. *Fisheries Research*, 62, 111–125.
- Milner, N. J., Solomon, D. J., & Smith, G. W. (2012). The role of river flow in the migration of adult Atlantic salmon, *Salmo salar*, through estuaries and rivers. *Fisheries Management and Ecology*, 19, 537–547.
- Montgomery, D. R., & Buffington, J. M. (1997). Channel-reach morphology in mountain drainage basins. *Geological Society of America Bulletin*, 109, 596–611.
- Moore, A., Bendall, B., Barry, J., Waring, C., Crooks, N., & Crooks, L. (2012). River temperature and adult anadromous Atlantic salmon, *Salmo salar*, and brown trout, *Salmo trutta*. *Fisheries Management and Ecology*, 19, 518–526.
- Morin, A., Rodriguez, M. A., & Nadon, D. (1995). Temporal and environmental variation in the biomass spectrum of benthic invertebrates in streams - an application of thin-plate splines and relative warp analysis. *Canadian Journal of Fisheries and Aquatic Sciences*, 52, 1881–1892.
- Myers, D. N. (2019). Innovations in monitoring with water-quality sensors with case studies on floods, hurricanes, and harmful algal blooms. In

- Ahuja Satinder *Separation science and technology* (pp. 219–283). Cambridge, MA: Academic Press.
- Nebeker, A. V. (1971). Effect of high winter water temperatures on adult emergence of aquatic insects. *Water Research*, 5, 777–783.
- Nicola, G. G., & Almodovar, A. (2004). Growth pattern of stream-dwelling brown trout under contrasting thermal conditions. *Transactions of the American Fisheries Society*, 133, 66–78.
- Nuhfer, A. J., Zorn, T. G., & Wills, T. C. (2017). Effects of reduced summer flows on the brook trout population and temperatures of a groundwater-influenced stream. *Ecology of Freshwater Fish*, 26, 108–119.
- Ojanguren, A. F., & Brana, F. (2003). Thermal dependence of embryonic growth and development in brown trout. *Journal of Fish Biology*, 62, 580–590.
- Ojanguren, A. F., Reyes-Gavilan, F. G., & Munoz, 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.
- Olden, J. D., Konrad, C. P., Melis, T. S., Kennard, M. J., Freeman, M. C., Mims, M. C., ... Lytle, D. A. (2014). Are large-scale flow experiments informing the science and management of freshwater ecosystems? *Frontiers in Ecology and the Environment*, 12, 176–185.
- Olden, J. D., & Naiman, R. J. (2010). Incorporating thermal regimes into environmental flows assessments: Modifying dam operations to restore freshwater ecosystem integrity. *Freshwater Biology*, 55, 86–107.
- Olsson, T. I. (1981). Overwintering of benthic macroinvertebrates in ice and frozen sediment in a north Swedish river. *Holarctic Ecology*, 4, 161–166.
- Olsson, T. I. (1983). Seasonal variation in the lateral distribution of mayfly nymphs in a boreal river. *Holarctic Ecology*, 6, 333–339.
- Ornsrud, R., Gil, L., & Waagbo, R. (2004). Teratogenicity of elevated egg incubation temperature and egg vitamin a status in Atlantic salmon, *Salmo salar* L. *Journal of Fish Diseases*, 27, 213–223.
- Ornsrud, R., Wargelius, A., Saele, O., Pittman, K., & Waagbo, R. (2004). Influence of egg vitamin a status and egg incubation temperature on subsequent development of the early vertebral column in Atlantic salmon fry. *Journal of Fish Biology*, 64, 399–417.
- Osterkamp, T., & Gosink, J. (1983). Frazil ice formation and ice cover development in interior Alaska streams. *Cold Regions Science and Technology*, 8, 43–56.
- Oswood, M. W., Miller, L. K., & Irons, J. G. (1991). Overwintering of freshwater benthic macroinvertebrates. In R. E. J. Lee & D. L. Denlinger (Eds.), *Insects at low temperature* (pp. 360–375). New York, NY: Chapman and Hall.
- Otero, J., L'Abée-Lund, J. H., Castro-Santos, T., Leonardsson, K., Storvik, G. O., Jonsson, B., ... Baglinière, J. L. (2014). Basin-scale phenology and effects of climate variability on global timing of initial seaward migration of Atlantic salmon (*Salmo salar*). *Global Change Biology*, 20, 61–75.
- Palmer, M. A., Lettenmaier, D. P., Poff, N. L., Postel, S. L., Richter, B., & Warner, R. (2009). Climate change and river ecosystems: Protection and adaptation options. *Environmental Management*, 44, 1053–1068.
- Pardo, I., Campbell, I., & Brittain, J. (1998). Influence of dam operation on mayfly assemblage structure and life histories in two south-eastern Australian streams. *Regulated Rivers: Research & Management*, 14, 285–295.
- Peel, M. C., Finlayson, B. L., & McMahon, T. A. (2007). Updated world map of the Köppen-Geiger climate classification. *Hydrology and Earth System Sciences Discussions*, 4, 439–473.
- Petrin, Z., Brittain, J. E., & Saltveit, S. J. (2013). Mayfly and stonefly species traits and species composition reflect hydrological regulation: A meta-analysis. *Freshwater Science*, 32, 425–437.
- Poff, N. L., & Zimmerman, J. K. (2010). Ecological responses to altered flow regimes: A literature review to inform the science and management of environmental flows. *Freshwater Biology*, 55, 194–205.
- Poole, G. C., & Berman, C. H. (2001). An ecological perspective on in-stream temperature: Natural heat dynamics and mechanisms of human-caused thermal degradation. *Environmental Management*, 27, 787–802.
- Portner, H. O. (2006). Climate-dependent evolution of Antarctic ectotherms: An integrative analysis. *Deep-sea research part II-topical studies in oceanography*, 53, 1071–1104.
- Portner, H. O. (2010). Oxygen- and capacity-limitation of thermal tolerance: A matrix for integrating climate-related stressor effects in marine ecosystems. *Journal of Experimental Biology*, 213, 881–893.
- Pörtner, H.-O. (2002). Physiological basis of temperature-dependent biogeography: Trade-offs in muscle design and performance in polar ectotherms. *Journal of Experimental Biology*, 205, 2217–2230.
- Prowse, T., Alfredsen, K., Beltaos, S., Bonsal, B. R., Bowden, W. B., Duguay, C. R., ... Weyhenmeyer, G. A. (2011). Effects of changes in Arctic Lake and river ice. *Ambio*, 40, 63–74.
- Prowse, T. D. (2001). River-ice ecology. II: Biological aspects. *Journal of Cold Regions Engineering*, 15, 17–33.
- Quinn, T. P., McGinnity, P., & Reed, T. E. (2016). The paradox of "premature migration" by adult anadromous salmonid fishes: Patterns and hypotheses. *Canadian Journal of Fisheries and Aquatic Sciences*, 73, 1015–1030.
- Raddum, G. G. (1985). Effects of winter warm reservoir release on benthic stream invertebrates. *Hydrobiologia*, 122, 105–111.
- Raddum, G. G., & Fjellheim, A. (1993). Life cycle and production of Baetis rhodani in a regulated river in Western Norway: Comparison of pre- and post-regulation conditions. *Regulated Rivers: Research & Management*, 8, 49–61.
- Raddum, G. G., Fjellheim, A., & Velle, G. (2008). Increased growth and distribution of *Ephemerella aurivillii* (Ephemeroptera) after hydropower regulation of the Aurland catchment in Western Norway. *River Research and Applications*, 24, 688–697.
- Reiser, D. W., & Wesche, T. A. (1979). In situ freezing as a cause of mortality in brown trout eggs. *The Progressive Fish-Culturist*, 41, 58–60.
- Renofalt, B. M., Jansson, R., & Nilsson, C. (2010). Effects of hydropower generation and opportunities for environmental flow management in Swedish riverine ecosystems. *Freshwater Biology*, 55, 49–67.
- Riedl, C., & Peter, A. (2013). Timing of brown trout spawning in alpine rivers with special consideration of egg burial depth. *Ecology of Freshwater Fish*, 22, 384–397.
- Rimmer, D. M., Paim, U., & Saunders, L. (1984). Changes in the selection of microhabitat by juvenile Atlantic salmon (*Salmo salar*) at the summer-autumn transition in a small river. *Canadian Journal of Fisheries and Aquatic Sciences*, 41, 469–475.
- Rishel, G. B., Lynch, J. A., & Corbett, E. S. (1982). Seasonal stream temperature changes following Forest harvesting. *Journal of Environmental Quality*, 11, 112–116.
- Rivers-Moore, N. A., Dallas, H. F., & Ross-Gillespie, V. (2013). Life history does matter in assessing potential ecological impacts of thermal changes on aquatic macroinvertebrates. *River Research and Applications*, 29, 1100–1109.
- Robards, M. D., & Quinn, T. P. (2002). The migratory timing of adult summer-run steelhead in the Columbia River over six decades of environmental change. *Transactions of the American Fisheries Society*, 131, 523–536.
- Roberts, J. H., Anderson, G. B., & Angermeier, P. L. (2016). A long-term study of ecological impacts of river channelization on the population of an endangered fish: Lessons learned for assessment and restoration. *Water*, 8, 240.

- Rolls, R. J., Leigh, C., & Sheldon, F. (2012). Mechanistic effects of low-flow hydrology on riverine ecosystems: Ecological principles and consequences of alteration. *Freshwater Science*, 31, 1163–1186.
- Ross-Gillespie, V., Picker, M. D., Dallas, H. F., & Day, J. A. (2018). The role of temperature in egg development of three aquatic insects *Lestagella penicillata* (Ephemeroptera), *Aphanicercella scutata* (Plecoptera), *Chimarra ambulans* (Trichoptera) from South Africa. *Journal of Thermal Biology*, 71, 158–170.
- Saltveit, S. J. (1990). Effect of decreased temperature on growth and smoltification of juvenile Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) in a norwegian regulated river. *Regulated Rivers: Research & Management*, 5, 295–303.
- Saltveit, S. J., & Brabrand, A. (2013). Incubation, hatching and survival of eggs of Atlantic salmon (*Salmo salar*) in spawning redds influenced by groundwater. *Limnologia*, 43, 325–331.
- Saltveit, S. J., Bremnes, T., & Brittain, J. E. (1994). Effect of a changed temperature regime on the benthos of a Norwegian regulated river. *Regulated Rivers-Research & Management*, 9, 93–102.
- Saltveit, S. J., Brittain, J. E., & Lillehammer, A. (1987). Stoneflies and river regulation. In J. F. Craig & J. B. Kemper (Eds.), *Regulated streams* (pp. 117–129). New York, NY: Plenum.
- Sanchez-Hernandez, J., Gabler, H. M., Elliott, J. M., & Amundsen, P. A. (2016). Use of a growth model to assess the suboptimal growth of Atlantic salmon parr in a subarctic river. *Ecology of Freshwater Fish*, 25, 518–526.
- Saraniemi, M., Huusko, A., & Tahkola, H. (2008). Spawning migration and habitat use of adfluvial brown trout, *Salmo trutta*, in a strongly seasonal boreal river. *Boreal Environment Research*, 13, 121–132.
- Sear, D. A., & DeVries, P. (2008). *Salmonid spawning habitat in Rivers: Physical controls, biological responses, and approaches to remediation*. Bethesda, MA: American Fisheries Society. <https://doi.org/10.47886/9781934874035>.
- Sertic Peric, M., & Robinson, C. T. (2015). Spatio-temporal shifts of macroinvertebrate drift and benthos in headwaters of a retreating glacier. *Hydrobiologia*, 751, 25–41.
- Sherman, B. (2000). *Scoping options for mitigating cold water discharges from dams*. CSIRO Land and Water Canberra. Consultancy Report 00/21, May 2000. https://www.researchgate.net/profile/Bradford-Sherman/publication/253447153_Scoping_Options_for_Mitigating_Cold_Water_Discharges_from_Dams/links/0deec5347621be003a000000/Scoping-Options-for-Mitigating-Cold-Water-Discharges-from-Dams.pdf
- Sherman, B., Todd, C. R., Koehn, J. D., & Ryan, T. (2007). Modelling the impact and potential mitigation of cold water pollution on Murray cod populations downstream of Hume dam, Australia. *River Research and Applications*, 23, 377–389.
- Shields, B. A., Stubbing, D. N., Summers, D. W., & Giles, N. (2005). Temporal and spatial segregation of spawning by wild and farm-reared brown trout, *Salmo trutta* L., in the river Avon, Wiltshire, UK. *Fisheries Management and Ecology*, 12, 77–79.
- Shuter, B. J., Finstad, A. G., Helland, I. P., Zweimuller, I., & Holker, F. (2012). The role of winter phenology in shaping the ecology of freshwater fish and their sensitivities to climate change. *Aquatic Sciences*, 74, 637–657.
- Skoglund, H., Einum, S., Forseth, T., & Barlaup, B. T. (2011). Phenotypic plasticity in physiological status at emergence from nests as a response to temperature in Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, 68, 1470–1479.
- Skoglund, H., Einum, S., Forseth, T., & Barlaup, B. T. (2012). The penalty for arriving late in emerging salmonid juveniles: Differences between species correspond to their interspecific competitive ability. *Functional Ecology*, 26, 104–111.
- Solomon, D. J., & Lightfoot, G. W. (2008). *The thermal biology of brown trout and Atlantic salmon*. Science Reports, Environment Agency, Rio House, Waterside Drive, Aztec West, Almondsbury, Bristol, BS32 4UD. p. 42. Retrieved from https://assets.publishing.service.gov.uk/government/uploads/system/uploads/attachment_data/file/291741/scho0808bolv-e-e.pdf
- 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.
- Staurnes, M., Sigholt, T., & Gulseth, O. A. (1994). Effects of seasonal changes in water temperature on the parr-smolt transformation of Atlantic salmon and anadromous Arctic char. *Transactions of the American Fisheries Society*, 123, 408–415.
- Stewart, D. C., Middlemas, S. J., & Youngson, A. F. (2006). Population structuring in Atlantic salmon (*Salmo salar*): Evidence of genetic influence on the timing of smolt migration in sub-catchment stocks. *Ecology of Freshwater Fish*, 15, 552–558.
- Stickler, M., & Alfredsen, K. T. (2009). Anchor ice formation in streams: A field study. *Hydrological Processes*, 23, 2307–2315.
- Stonecypher, R. W., Hubert, W. A., & Gern, W. A. (1994). Effect of reduced incubation temperatures on survival of trout embryos. *The Progressive Fish-Culturist*, 56, 180–184.
- Sunday, J., Bennett, J. M., Calosi, P., Clusella-Trullas, S., Gravel, S., Hargreaves, A. L., ... Morales-Castilla, I. (2019). Thermal tolerance patterns across latitude and elevation. *Philosophical Transactions of the Royal Society B*, 374, 20190036.
- Svensson, P.-O. (1966). Growth of nymphs of stream living stoneflies (Plecoptera) in northern Sweden. *Oikos*, 17, 197–206.
- Syrjanen, J., Kiljunen, M., Karjalainen, J., Eloranta, A., & Muotka, T. (2008). Survival and growth of brown trout *Salmo trutta* L. embryos and the timing of hatching and emergence in two boreal lake outlet streams. *Journal of Fish Biology*, 72, 985–1000.
- Takle, H., Baeverfjord, G., & Andersen, O. (2004). Identification of stress sensitive genes in hyperthermic Atlantic salmon (*Salmo salar*) embryos by RAP-PCR. *Fish Physiology and Biochemistry*, 30, 275–281.
- Takle, H., Baeverfjord, G., Helland, S., Kjorsvik, E., & Andersen, O. (2006). Hyperthermia induced atrial natriuretic peptide expression and deviant heart development in Atlantic salmon *Salmo salar* embryos. *General and Comparative Endocrinology*, 147, 118–125.
- Taranger, G. L., & Hansen, T. (1993). Ovulation and egg survival following exposure of Atlantic salmon, *Salmo salar* L., broodstock to different water temperatures. *Aquaculture Research*, 24, 151–156.
- Tauro, F., Selker, J., Van De Giesen, N., Abrate, T., Uijlenhoet, R., Porfiri, M., ... Benveniste, J. (2018). Measurements and observations in the XXI century (MOXXI): Innovation and multi-disciplinarity to sense the hydrological cycle. *Hydrological Sciences Journal*, 63, 169–196.
- 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.
- Thorstad, E. B., Okland, F., Aarestrup, K., & Heggberget, T. G. (2008). Factors affecting the within-river spawning migration of Atlantic salmon, with emphasis on human impacts. *Reviews in Fish Biology and Fisheries*, 18, 345–371.
- Timalsina, N. P., Alfredsen, K. T., & Killingtveit, A. (2015). Impact of climate change on ice regime in a river regulated for hydropower. *Canadian Journal of Civil Engineering*, 42, 634–644.
- Timalsina, N. P., Charmasson, J., & Alfredsen, K. T. (2013). Simulation of the ice regime in a Norwegian regulated river. *Cold Regions Science and Technology*, 94, 61–73.
- Toffolon, M., Siviglia, A., & Zolezzi, G. (2010). Thermal wave dynamics in rivers affected by hydropowering. *Water Resources Research*, 46 (8), 1–18.
- Turcotte, B., & Morse, B. (2013). A global river ice classification model. *Journal of Hydrology*, 507, 134–148.
- Tvede, A. (2006). *Vanntemperatur og isforhold*. Økologiske Forhold i Vassdrag-Konsekvenser Av vannføringsendringer. En Sammenstilling

- Av Dagens Kunnskap, pp. 27–34. Retrieved from <http://publikasjoner.nve.no/diverse/2006/oekologiskeforholdivassdrag2006.pdf>
- Tvede, A. M. (1994). Discharge, water temperature and glaciers in the Aurland river basin. *Norsk Geografisk Tidsskrift-Norwegian Journal of Geography*, 48, 23–28.
- Ugedal, O., Naesje, T. F., Thorstad, E. B., Forseth, T., Saksgard, L. M., & Heggberget, T. G. (2008). Twenty years of hydropower regulation in the river Alta: Long-term changes in abundance of juvenile and adult Atlantic salmon. *Hydrobiologia*, 609, 9–23.
- Valdimarsson, S. K., & Metcalfe, N. B. (2001). Is the level of aggression and dispersion in territorial fish dependent on light intensity? *Animal Behaviour*, 61, 1143–1149.
- Vannote, R. L., Minshall, G. W., Cummins, K. W., Sedell, J. R., & Cushing, C. E. (1980). River continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, 37, 130–137.
- Vannote, R. L., & Sweeney, B. W. (1980). Geographic analysis of thermal equilibria - a conceptual-model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. *American Naturalist*, 115, 667–695.
- Vanzo, D., Siviglia, A., Carolli, M., & Zolezzi, G. (2016). Characterization of sub-daily thermal regime in alpine rivers: Quantification of alterations induced by hydropowering. *Hydrological Processes*, 30, 1052–1070.
- Vanzo, D., Tancon, M., Zolezzi, G., Alfredsen, K. & Siviglia, A. (2016). A modeling approach for the quantification of fish stranding risk: The case of Lundesokna River (Norway). Paper presented at: Proceedings from the 11th International Symposium on Ecohydraulics (ISE 2016). Engineers Australia pp. 326–333. Retrieved from <https://search.informit.org/doi/10.3316/informit.687014727486689>
- Vermeyen, T. (2000). *Application of flexible curtains to control mixing and enable selective withdrawal in reservoirs*. IAHR, Proceedings from the 5th International Symposium on Stratified Flows, Vancouver, Canada. Retrieved from <http://www.project2105.org/TC/PAP-0847.pdf>
- Vikingstad, E., Andersson, E., Hansen, T. J., Norberg, B., Mayer, I., Stefansson, S. O., ... Taranger, G. L. (2016). Effects of temperature on the final stages of sexual maturation in Atlantic salmon (*Salmo salar* L.). *Fish Physiology and Biochemistry*, 42, 895–907.
- Vikingstad, E., Andersson, E., Norberg, B., Mayer, I., Klenke, U., Zohar, Y., ... Taranger, G. L. (2008). The combined effects of temperature and GnRHa treatment on the final stages of sexual maturation in Atlantic salmon (*Salmo salar* L.) females. *Fish Physiology and Biochemistry*, 34, 289–298.
- Vinson, M. R. (2001). Long-term dynamics of an invertebrate assemblage downstream from a large dam. *Ecological Applications*, 11, 711–730.
- Wallace, J. C., & Heggberget, T. G. (1988). Incubation of eggs of Atlantic salmon (*Salmo salar*) from different Norwegian streams at temperatures below 1-degrees-c. *Canadian Journal of Fisheries and Aquatic Sciences*, 45, 193–196.
- Ward, J. (1994). Ecology of alpine streams. *Freshwater Biology*, 32, 277–294.
- Ward, J. V., & Stanford, J. (1982). Thermal responses in the evolutionary ecology of aquatic insects. *Annual Review of Entomology*, 27, 97–117.
- Ward, J. V., & Stanford, J. A. (1979). Ecological factors controlling stream zoobenthos with emphasis on thermal modification of regulated streams. In *The ecology of regulated streams* (pp. 35–55). Boston: Springer.
- Waringer, J. A. (1992). The drifting of invertebrates and particulate organic-matter in an Austrian mountain brook. *Freshwater Biology*, 27, 367–378.
- Webb, B., & Walling, D. (1988). Modification of temperature behaviour through regulation of a British river system. *River Research and Applications*, 2, 103–116.
- Webb, B., & Walling, D. (1993). Temporal variability in the impact of river regulation on thermal regime and some biological implications. *Freshwater Biology*, 29, 167–182.
- Webb, B., & Walling, D. (1997). Complex summer water temperature behaviour below a UKregulating reservoir. *River Research and Applications*, 13, 463–477.
- Webb, B. W., Hannah, D. M., Moore, R. D., Brown, L. E., & Nobilis, F. (2008). Recent advances in stream and river temperature research. *Hydrological Processes*, 22, 902–918.
- Webb, J. H., & McLay, H. A. (1996). Variation in the time of spawning of Atlantic salmon (*Salmo salar*) and its relationship to temperature in the Aberdeenshire Dee, Scotland. *Canadian Journal of Fisheries and Aquatic Sciences*, 53, 2739–2744.
- Weber, C., Nilsson, C., Lind, L., Alfredsen, K. T., & Polvi, L. E. (2013). Winter disturbances and riverine fish in temperate and cold regions. *Bioscience*, 63, 199–210.
- White, J. C., Hannah, D. M., House, A., Beatson, S. J. V., Martin, A., & Wood, P. J. (2017). Macroinvertebrate responses to flow and stream temperature variability across regulated and non-regulated rivers. *Ecohydrology*, 10, e1773.
- Woodward, G., Perkins, D. M., & Brown, L. E. (2010). Climate change and freshwater ecosystems: Impacts across multiple levels of organization. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365, 2093–2106.

How to cite this article: Heggenes J, Stickler M, Alfredsen K, Brittain JE, Adeva-Bustos A, Huusko A. Hydropower-driven thermal changes, biological responses and mitigating measures in northern river systems. *River Res Applic*. 2021;37:743–765. <https://doi.org/10.1002/rra.3788>