




REVIEW PAPER

WILEY

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

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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

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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.

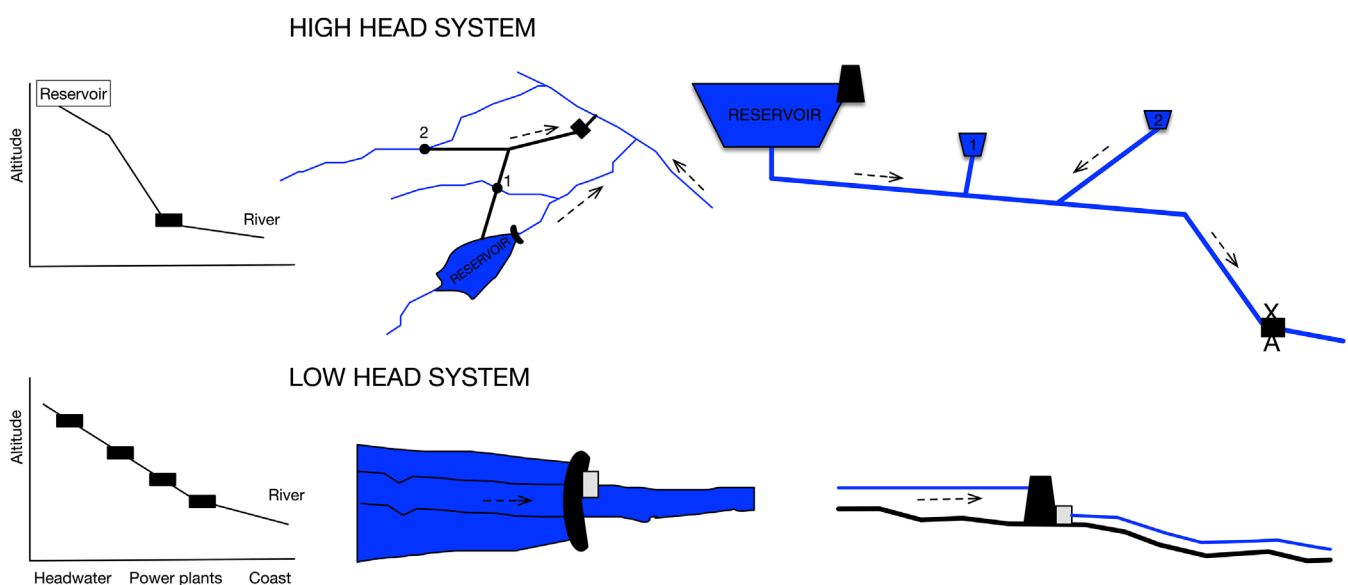


FIGURE 1 The two typical hydropower regulation systems. Top: a high head system with a high elevation reservoir, tributary intakes, and transfer tunnels to the power plant, which could also include a pumped storage facility. Bottom: a low head or run-of-the-river mainstem system with intake and power 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.

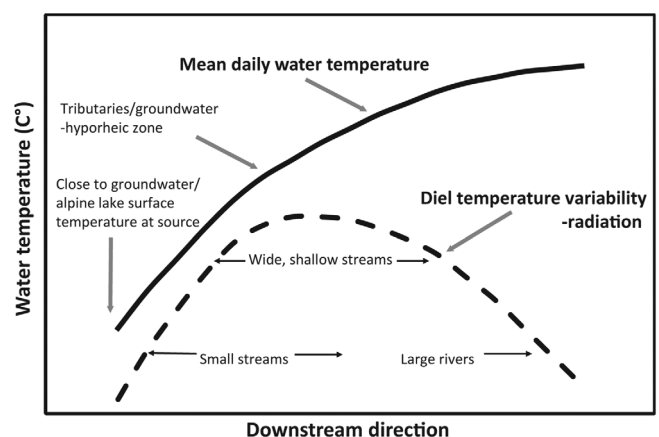


FIGURE 2 Schematic representation of mean daily and diel water temperature variability as a function of spatial scale, that is, downstream direction, which also generally translates to stream order. (Modified after Caissie, 2006; Austin et al., 2015)

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

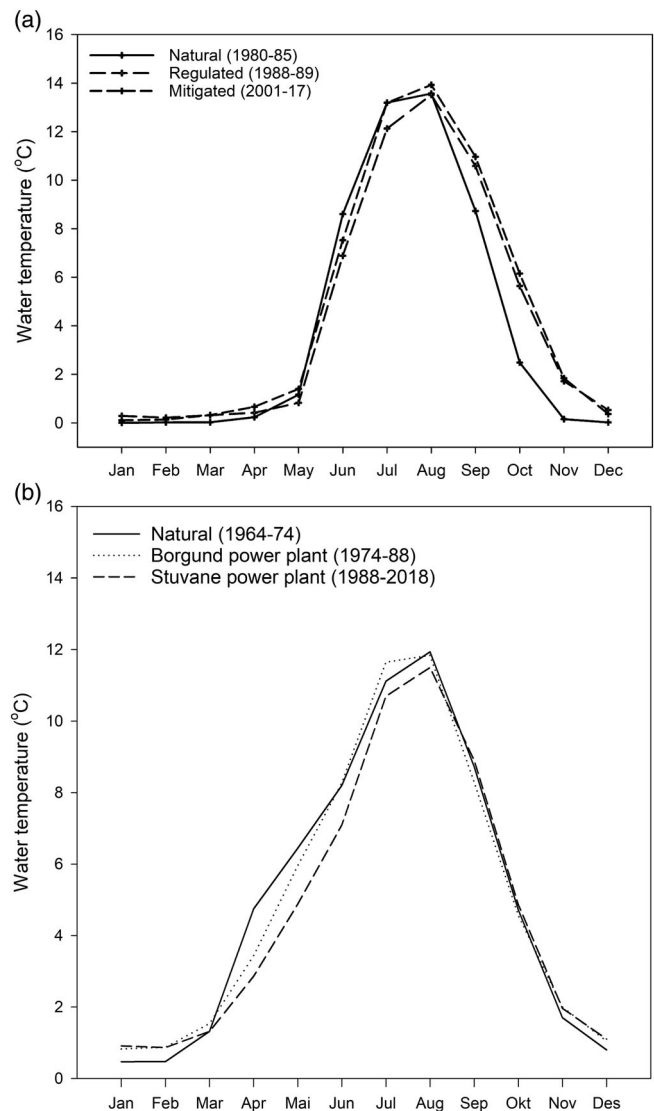


FIGURE 3 (a) Mean monthly water temperatures for Alta River, North-Norway, were raised 1–2°C primarily in fall–winter from before to after regulation. The effect was reduced somewhat after restoration/mitigation, primarily to obtain more surface ice cover in winter. (b) Mean monthly water temperatures 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

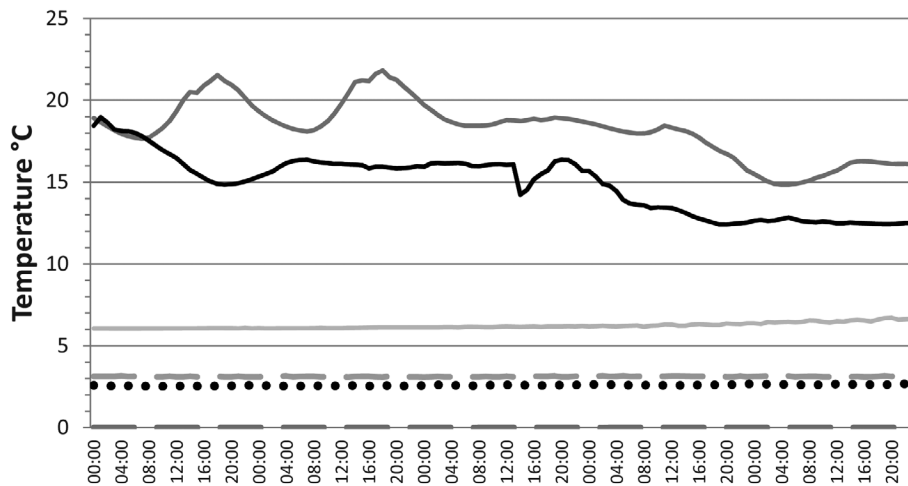


FIGURE 4 Typical winter (bottom dashed lines) and summer (top solid lines) water temperature changes effected by high head hydropower regulation (January and July 2009, Vallaråi R., South-East Norway). Winter: Upstream residual flow water with temperature about 0°C (lower dashed dark grey line) is mixed 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, & Timalina, 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; Huryñ & 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 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, photoperiod), 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

<p>Hydro-physical conditions</p> <p>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?</p> <p>How do different production regimes (e.g., peaking or seasonal) affect longitudinal downstream water temperatures?</p> <p>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?</p> <p>To what extent do different macroinvertebrates survive encasement in ice?</p> <p>Is egg survival and invertebrate production higher in “winter-warm” regulated rivers than in the natural state?</p> <p>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?</p>
<p>Biological responses</p> <p>Longitudinal water temperature impacts on fish populations and invertebrate communities at the river scale?</p> <p>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?</p>
<p>Mitigating measures</p> <p>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?</p> <p>What are the effects of hydropower regulation-induced temperature changes/increases in early spring on egg and alevin development and survival?</p> <p>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?</p> <p>Regarding models, development and integration of small-scale thermal (fish) habitat models and validation against fish data, are also remaining challenges.</p>

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 4–5°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 Heggnes, 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 (Heggnes, 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 0–3°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, & Timalina, 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

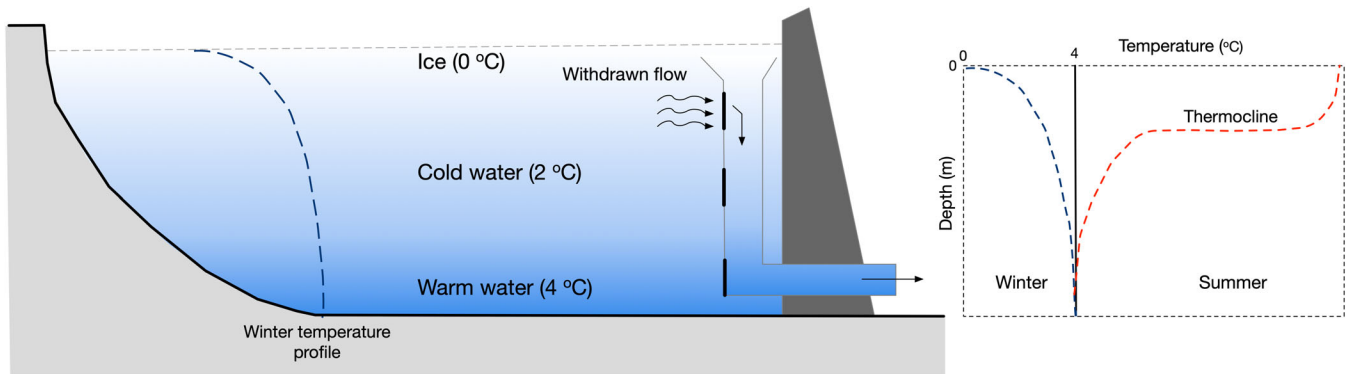


FIGURE 5 Intake control of temperature: multi-level intake structure makes use of the stratification within the reservoir by permitting water with desirable thermal attributes (in this case winter condition, therefore upper layer) to be withdrawn from defined regions within the water column. (Modified 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.

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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;1–23. <https://doi.org/10.1002/rra.3788>