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responses in hydropower-regulated
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Abstract

In the seasonal climates of northern Europe and North America, water temperature variations are ecologically challenging for aquatic organisms in natural streams. In winter, low water temperature and ice conditions becall biological responses by aquatic species, whereas in summer water temperatures rise and may, in particular during daytime low flows, approach lethal levels. In ectothermic animals, like the cold-water fish Atlantic salmon and brown trout, and the benthic fauna, biochemical reactions and behaviors depend on water temperature. As many northern rivers are impacted by hydropower regulation, natural water temperature regimes are potentially altered. Typically, low head (run-of-the-river) regulation has limited impacts on water temperatures, but depending on the, usually limited, water storage capacity. In contrast, high head hydropower regulation systems have considerable water storage capacity in reservoirs. This alters downstream water temperatures, typically with an increase in winter (tapped from warm bottom water (below thermocline) in reservoir), and a decrease in summer (bottom water being colder than natural surface water). Thus, the naturally stable, ice-covered mid-winter periods may be replaced by repeated unstable transition periods and changing (or no) ice and flood conditions, whereas in summer, (downstream) water temperatures may be lowered when the hydropower plant is in operation. Conversely, by-pass reaches and reaches with reduced residual or environmental minimum flows during water storage, are more prone to fluctuate with environmental temperatures. In summer, this may lead to higher day-night and seasonal water temperatures and amplitudes, and lower and more frequent sub-zero temperatures in winter. However, the effects of alternative regulation regimes and reservoir intakes/outlets on downstream ambient temperatures are not well publicized. Hydro-peaked systems may aggravate high-low temperature effects, depending on flow regime (ramping rate and amplitude, frequency of flow fluctuations, prior flow conditions, timing of pulse).

Atlantic salmon and brown trout feeding and growth performance in summer (and transient periods) depend primarily on water temperatures (above ≈ 3-4°C, optimum ≈ 13-16°C). At high temperatures, and approaching tolerance limits (≈ 22-24°C), trout and salmon reduce and cease feeding, and may move into cooler water in the substrate or groundwater inflow. Larger fish may move more and aggregate in restricted suitable deep-slow or cool refuge habitats, both in summer and winter. In winter, feeding and growth in typically absent, and energy storage is the basic fish low temperature survival strategy. Additional strategies may be risk reduction effected by behavioral changes, and

reduced metabolism, tolerance and starvation effected by quiescence. Amount of energy stored may depend on local conditions, but otherwise there is hitherto little indication of adaptation to local thermal climates. However, phenotypic plasticity is important and substantial. The main behavioral strategy at low water temperatures (less than 6-8°C) is risk-reducing daytime sheltering in the substrate and primarily nocturnal activity. In winter, mechanical ice breakups may still reduce survival. Moreover, sudden drops in water flow due to hydropeaking may result in fish stranding, in particular at low temperatures in the daytime when fish are less mobile and seek shelter. Local movements between daytime refuges and nighttime activity areas occur both at low and high temperatures. Water temperature and/or flow may control more local spawning/smolt migrations, particularly in smaller streams. Fish egg development is also closely linked to water temperature. Emerging alevins and young fry are sensitive and vulnerable, often incurring high mortalities. Survival may depend on a delicate balance between temperature, suitable low flows and available drifting food during and after the 'swim-up' stage.

Benthic macroinvertebrates display various strategies for dealing with high summer temperatures and low winter temperatures coupled with ice formation. Growth temperatures tend to be species specific, and as a group benthic macroinvertebrates exhibit growth across a wide temperature range. Some species are adapted to high summer temperatures, while others undergo quiescence or diapause, most commonly in the egg stage, in order to avoid such unfavorable periods. Likewise, other species avoid unfavorable periods during winter by quiescence or diapause. Another strategy, which can be coupled with diapause/quiescence, is to move down into the substrate, even into the hyporheic, especially in groundwater-fed areas. A further strategy is to undertake seasonal movements, either into tributaries or into deeper ice-free river waters. However, certain species, notably Diptera, but also other orders, have been shown to tolerate freezing – a stay-put strategy. Modified water temperatures may have major effects on life cycles, and even lead to extinction of specialist species, as many facets of growth and emergence are affected by or cued by temperature. Benthic species that have a rigid synchronous one year or univoltine life cycles are most at risk, while species with flexible and asynchronous life cycles will be favored. A reduction in the temperature range between winter and summer will lead to a reduction in species richness, again favoring the widespread, ubiquitous species. Nevertheless, most benthic organisms have high fecundity which may be offset high mortality during the different life cycle stages.

Knowledge about thermal changes caused by hydropower regulation, and associated biological impacts on aquatic species, is a prerequisite for sustainable management of regulated rivers. In ongoing revisions of environmental guidelines and terms for hydropower regulated river systems, thermal changes and impacts have gained central focus. Thermal considerations will continue to be a key for setting future environmental flows and mitigation strategies. However, quantitative and observational knowledge is rather limited, whereas theoretical assumptions and modelling are more developed. Therefore, *in situ* target-oriented investigations in combination with more general research programs on water temperature changes, is essential, both from an operators (reduce costs and production losses) and managers perspective (fact-based knowledge and environmental guidelines). Based on this review, we recommend some main topics for further knowledge development: i) general quantitative knowledge on thermal changes due to hydropower regulation; ii) longitudinal water temperature changes from power outlet and in minimum flow reaches; iii) biological effects of reduced winter snow and ice cover, and increased frazil ice production, iv) invertebrate production in winter-warm rivers, and v) thermal adaptations to changed thermal regimes. With respect to mitigating measures, more knowledge is needed on i) effects of restored/increased minimum flows on invertebrate and fish composition, survival and production, ii) effects of changed/restored thermal regime, e. g. by installing multiple intakes in reservoirs, iii) empirical studies to test and validate the predictions of the at present quite well-developed hydro-hydraulic models. Because of the substantial background variation in river systems, long-term studies are of particular importance.

Contents

1. INTRODUCTION

"Among gill-respiring vertebrates there is no escape from environmental temperature" (Brett 1956).

Climate **determines** water temperatures in streams. The 21st century predicted anthropogenic winter climate change in northern Europe and North America is warmer, wetter and stormier weather, with more frequent extreme events, e.g. flooding and rain-on-snow events, and less snow (IPCC 2014; Shanley *et al.* 2015). Thermal regimes in many seasonal streams and lakes in Northern Europe and Northern America are also impacted by hydropower regulation in ways that may resemble projected climate changes (Prowse *et al.* 2011; van Vliet, Ludwig & Kabat 2013; Gebre, Timalsina & Alfredsen 2014), e.g. if changed, regulated water courses tend to be warmer (Webb & Walling 1996; Moore 2006; Webb *et al.* 2008b). With an installed capacity of 100 GW or more in the northern countries (Prowse *et al.* 2011; Anonymous 2016), hydropower development is extensive, and temperatures in most running waters are modified by hydropower regulation. For example, in Norway with 97% hydropower of total energy production, two-thirds of all watersheds are regulated, presumably with modified temperature regimes, and they contribute about 50% of total reservoir capacity in Europe. A main effect in freshwater thermal regimes due to hydro-regulation is changed timing and magnitude (e.g. Webb & Walling 1997; Asvall 2005; Kvambekk 2012; Gillespie *et al.* 2015). Indeed, although effects are likely to be complex and site-specific (Poff & Zimmerman 2010; Gillespie *et al.* 2015), decrease in inter-annual and intra-annual variability is typical for most elements of the regulated flow regime (Renofalt, Jansson & Nilsson 2010; Geris *et al.* 2015). It depends on amount and thermal inertia of stored water, development of thermal stratification, release depths, release flows relative to residual flows, groundwater, and catchment characteristics (e.g. Moore 2006; Webb *et al.* 2008b). Bypass reaches may be different, often with increased temperature amplitudes, but depending on environmental flows. The biological implications of such thermal changes are important, and organisms may suffer or benefit from temperature regimes modified by hydropower (Poole & Berman 2001; Poff & Zimmerman 2010).

In ectothermic freshwater animals, natural seasonal water temperatures may be the most pervasive environmental factor determining their lives. The rates of biochemical reactions, ontological development and behavioral responses, depend on water temperature, e.g. for widely distributed and culturally important cold-water fish like Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) (Angilletta, Niewiarowski & Navas 2002; Elliott & Elliott 2010; Dell, Pawar & Savage 2011). Also, in most aquatic macroinvertebrates egg development and growth are temperature related and their rates increase with increasing temperature until sub-optimal temperatures are reached (Ward & Stanford 1982; Sweeney 1984; Brittain 1990). However, a few cold adapted macroinvertebrate species display temperature independent growth (Brittain 1983; Brittain, Lillehammer & Saltveit 1986). High summer or low winter temperatures generate thermal stress and challenge physiological tolerances, and may reach lethal levels particularly in summer. Lower summer temperatures that lead to reduced growth, although not lethal, can lead to extinction on account of competitive disadvantage (Edington & Hildrew 1973). Thermal stress may be mitigated by basal thermo-tolerance, but also by more adaptive plastic responses like acclimation and behavioral adjustments. In seasonal climates, fitness may reflect the ability of ectothermic organisms like fish and warm-adapted macroinvertebrates, such as those with a long egg development period during winter and rapid growth during late spring and summer, to exploit the favorable summer season for temperature-dependent recruitment and growth. It may also reflect developmental, physiological and behavioral strategies to mitigate the effects of the unfavourable low temperature season (Bradshaw, Zani & Holzapfel 2004; Hedger *et al.* 2013d). In winter, water temperatures drop as low as freezing (≤0°C), incurring ice formation (Prowse 2001; Turcotte & Morse 2013), and additional stress in streams by direct hydro-physical changes. Ice phenomena have, however, been reviewed in a previous report (Heggenes *et al.* 2016). The present report focuses on water temperatures.

Thus, in the typical seasonal climates of northern Europe and North America, the balance between length and intensity of the low and high temperature seasons is pervasively important in stream systems. The 21st century predicted shorter and more unstable winters and longer and warmer summers in streams (e.g. Graham & Harrod 2009; Jonsson & Jonsson 2009; Heino *et al.* 2016), will have cascading ecosystem-level effects, including shrinking alpine/arctic habitats and magnitude and timing of freshwater thermal regimes (Shanley *et al.* 2015). This

scenario will likely have severe consequences for cold-water fish and benthic animals including Atlantic salmon and brown trout (Brown, Hannah & Milner 2007; Jonsson & Jonsson 2009; Crozier & Hutchings 2014).

What is theory, what is researched, and what do we know that can be applied towards industrial solutions? Recent reviews of ecological responses have focused on the more obvious direct flow changes associated with regulated rivers (Poff & Zimmerman 2010; Olden *et al.* 2014; Gillespie *et al.* 2015) (but see Austin *et al.* 2015). Even so, analysis' were restricted by both small number of data points and limited information. Furthermore, Gillespie *et al.* (2015) noted that temperature studies were few and 'Further research should be directed towards assessment of the relative importance of different flow modification types in controlling downstream temperature,…'. Therefore, the objective of this paper is to focus on (1) how hydropower regulation may impact seasonal water temperatures, and thereby (2) different life stages of relevant freshwater organisms, and (3) their responses to tackle temperature changes with associated ecological consequences, and (4) potential good practices to mitigate effects of hydropower related temperature changes in regulated streams. We first briefly consider important natural water temperature processes and patterns in natural stream systems, as a background to understand how hydropower regulation may influence these processes and patterns. We then consider how fish and stream macroinvertebrates have been found to respond to such hydropower- generated changes in their stream environments, and how we can learn from these responses and use that knowledge as a basis for improved environmental friendly practices in regulated streams and rivers.

2. WATER TEMPERATURE PROCESSES IN NATURAL STREAM SYSTEMS

Freshwater organisms are adapted to their natural stream environments, and any responses to hydropower impacts will therefore, reflect their repertoire of natural responses to environmental dynamic changes. Because thermal regimes show strong seasonal variation in Northern Europe and Northern America, there are marked seasonal variation and patterns in the natural aquatic environment experienced by aquatic organisms. Some physical properties

of water, in particular density, also depend on temperature. These water density changes generate important seasonal patterns in particular in lakes (and reservoirs), referred to as thermal stratification. Such thermal stratification tend be relatively stable during summer and winter, but with marked changes during the transient periods with marked temperature changes in spring and autumn. In broad terms, lakes (and reservoirs) constitute a large body of water with a high thermal capacity, lower surface to volume ratio and longer retention time compared to a stream (e.g. Petts 1986; Austin *et al.* 2015).

2.1. Transient periods and seasonal lake thermal stratification

Cooling changes the physical properties of water. Decreasing temperatures in fall make water denser, but with a maximum water density around 4°C. Thus, warming in early spring will also make water denser up to 4°C (Fig. 1). In northern lakes, this means a seasonal cyclical pattern of total water mixing (wind-sensitive overturns) during the transient spring and fall periods when all water reaches 4°C, and have the same density (Fig. 1). The summer thermal stratification arises as surface water warms up. It is therefore characterized by a colder and denser bottom *hypolimnion* at 4°C, a usually abrupt *thermocline* and a warmer and less dense top *epilimnion* (Fig.1). This warmer epilimnion layer will increase in depth through the spring and into early summer (Fig. 1) (e.g. Maberly 1996). With decreasing surface temperatures in the fall, colder and therefore denser water sinks, eventually causing a fall turnover. The lake then enters the winter thermal stratification, with an about 4°C bottom winter stagnation hypolimnion, with a typically thin top layer of colder water under the stabilizing surface ice that prevents disturbing wind action. There are associated changes in water chemistry (e.g. Maberly 1996), notably turnovers transport oxygen to the bottom layers and nutrients the opposite way, affecting e.g. carbon and pH. The specific development of such thermal stratification in lakes and reservoirs depends on lake and reservoir characteristics (e.g. depth, surface/volume ratio, wind exposition, inflow/outflow/retention time).
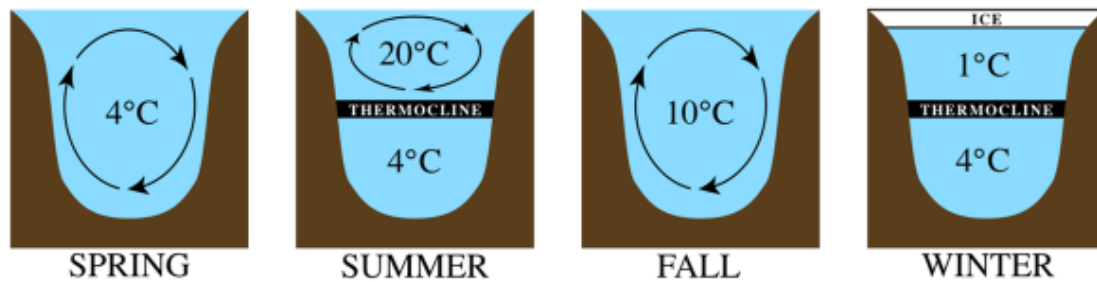
Figure 1. Temperature-driven stratification in lakes.

Although lakes and reservoirs may have similarities with respect to limnological processes, there are some notable difference (Petts 1986; Poole & Berman 2001; Austin *et al.* 2015):

- ✓ Reservoirs are constructed to maximize water storage and minimize land area impounded, and thus may have smaller surface area/volume ratios, i.e. less influenced by wind and surface heat transfer,
- ✓ Reservoir water surfaces are variable, i.e. more vertical heat mixing and advective heat transfer,
- ✓ Release of reservoir water can be at any depth, but typically deeper than natural lakes which is almost always from the surface, i.e. changes reservoir water movement and release temperatures,
- ✓ Reservoir release thus influence downstream water flow and quality directly (see next chapters),
- ✓ and indirectly, via influencing processes that control delivery, distribution and retention of heat and chemically, affecting for example ice formation (see next chapters).

Such thermal stratification typically does not occur in running waters because of turbulence, except perhaps locally in stillwater side channels and deep pools. Moreover, natural streams flowing out of lakes are fed from the epilimnion. In regulated streams, however, this may be radically different (see ch. 4).

2.2. Winter cold and ice in streams

During the cold season in winter, low temperatures *per se* may challenge organisms and infer thermal stress (Angilletta, Niewiarowski & Navas 2002; Elliott & Elliott 2010; Gerken *et al.* 2015). However, what really will change the hydro-physical winter conditions in streams and rivers, are the presence and length of periods of freezing temperatures that immobilize water as ice. Whereas surface ice tend to stabilize conditions in lakes (e. g. Hutchinson & Löffler 1956; Hampton *et al.* 2017), ice phenomena in streams may precipitate hydro-physical habitat changes that challenge organisms (Prowse & Ommanney 1990; Prowse 2001; Huusko *et al.* 2007; Huusko, Vehanen & Stickler 2013). Moreover, the complex production of a diversity of ice types may vary depending on very small changes in water temperatures, a hundredth degree in supercooled water (Fig. 2) (Stickler & Alfredsen 2009), and also hydraulics in ice-free areas. These patterns may be modified considerably by hydropower regulation (Stickler & Alfredsen 2009; Gebre *et al.* 2013). Ice-cover types and processes (see Turcotte & Morse 2013 for details) also profoundly affect functional stream environments for organisms, detailed in a previous report (Heggenes *et al.* 2016).
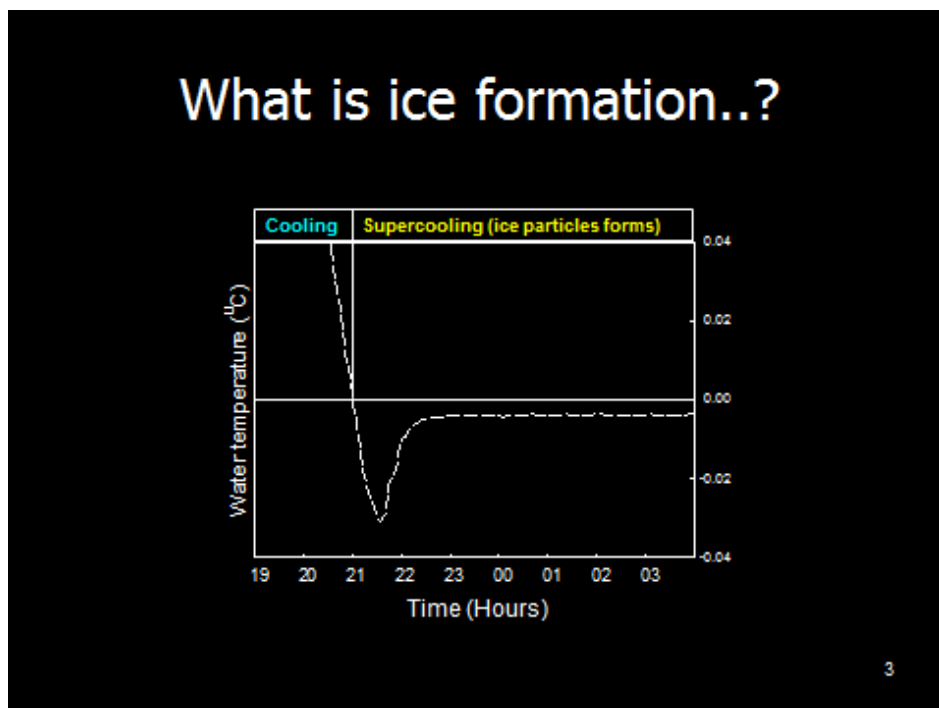
Figure 2. Ice formation in water occur when water temperature drops below 0 °C. Super cooled water occur within short time frames, and ice formation may happen almost instantly.

2.3. Summer warming and stream temperature gradients

In lakes, after spring overturn with water temperatures around 4°C, the summer thermal stratification develops with increasing temperatures, with its colder and denser hypolimnion at 4°C, a the thermocline, and a warmer and less dense epilimnion as the lake heats from the surface down. As spring and summer progress, the epilimnion stratum gains more depth, eventually reaching a maximum depth maintained for the remainder of the summer (Fig. 1). Turbulence mixes water in streams, which typically do not exhibit thermal stratification, but stream temperatures typically resembles that of the watershed's heat radiation regime and subsoil environment, broadly determined by atmospheric conditions, topography, streambed, and stream discharge (Caissie 2006a). Fundamental temperature controls of non-advective heat input in streams are radiative fluxes, often the most important (maybe as much as ca. 70%), but also water friction with the bed and the banks, and sensible heat transfer from the atmosphere. Main heat outputs are net radiation, evaporation, bed conduction, and sensible heat transfer to the atmosphere (Webb *et al.* 2008b). This may be modified by the environment, for example topographic shading or presence of forest canopy, or exchange of water with the hyporheic environment (Poole & Berman 2001; Caissie 2006a). Stream temperature 'micro'gradients (cm to meters; Webb *et al.* 2008b) tend to be limited, and if found, related to strong solar heating and low flows, inflows from a range of sources with different thermal characteristics, notably meltwater, groundwater or tributaries, or lake outflows (e.g. Nuhfer, Zorn & Wills 2017). Thus streams often heat or cool primarily by radiation to or from the surface (e.g. Rishel, Lynch & Corbett 1982; Caissie 2006a). Thermal complexity and heterogeneity may be considerable, particularly in alpine streams (Ward 1994a; Brown, Hannah & Milner 2006; Cadbury *et al.* 2008). Environmental temperatures in conjunction with surface area relative to volume largely determine stream temperatures, with the smaller, wider, shallower streams responding more rapidly. Therefore, on a spatial scale, stream temperatures tend to increase with lower altitudes downstream, but modified by e.g. groundwater and tributary inflows (Fig. 3a). This is also reflected on a temporal scale, with diel, annual and inter-annual temperature variation more pronounced in smaller streams (Fig. 3a, 3b). For example, temperatures may vary markedly between day and night, particularly in small, shallow, wide streams, as in a bypass or residual flow stream reach (Fig. 3b).
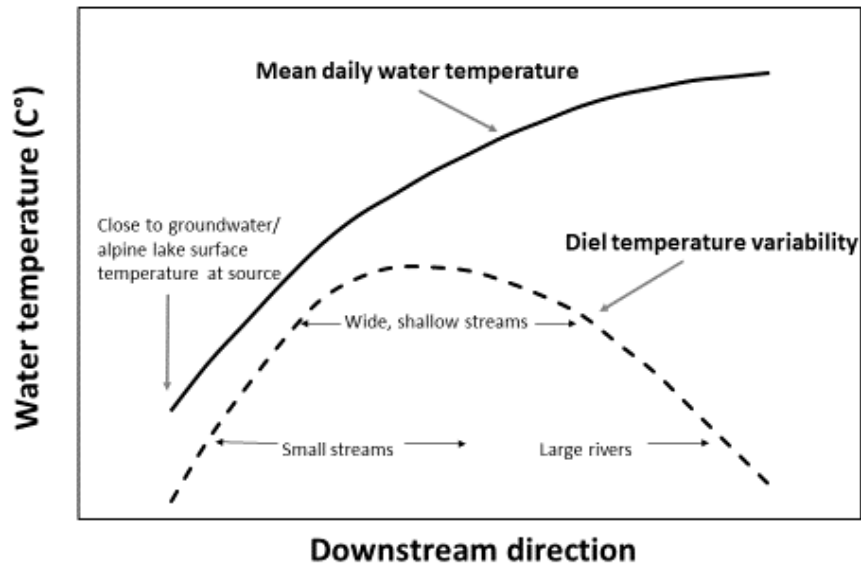
Fig. 3a. Schematic representation of mean daily and diel water temperature variability as a function of spatial scale, i.e. downstream direction, which also generally translates to stream order. Modified from (Caissie 2006a; Austin et al. 2015)
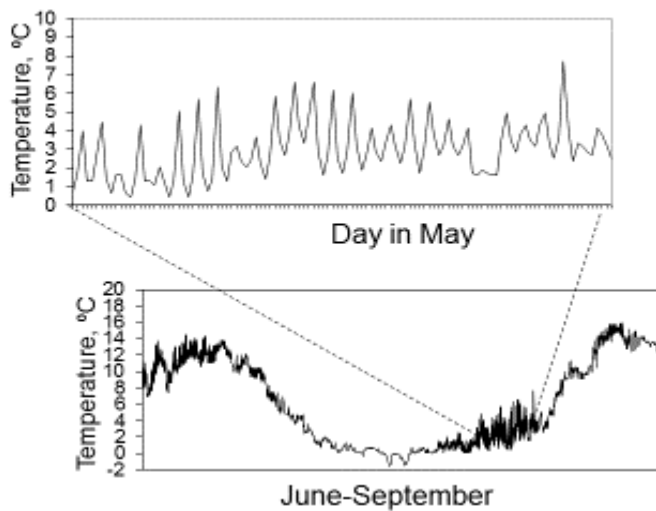
Fig. 3b. Annual and day-night temperature variation in streams. Stream temperatures from June 1998 to September 1999 in the regulated river Måna R, Norway. During a period in May 1999 with residual flow only, daily temperature amplitudes increase dramatically.

3. HYDROPOWER REGULATION IMPACTS ON WATER TEMPERATURE IN STREAM SYSTEMS

The natural seasonal stream temperatures are often modified considerably by hydropower regulation through changing the amount and/or timing of water delivered, particularly in reaches downstream of power-plant outlets (Fig. 4). Here we first consider two main types of hydropower regulation and their different effects on water temperatures before we review how they may change the natural seasonal temperatures patterns in stream systems. In winter in many such rivers, the naturally near 0°C water and stable mid-winter periods (surface ice cover) may be replaced by warmer water and repeated unstable transition periods (Fig. 4) (Stickler & Alfredsen 2009; Prowse *et al.* 2011; Gebre *et al.* 2013; Weber *et al.* 2013). In summer, warmer water heated by solar radiation may be replaced by cooler water drawn from deep reservoirs (Fig. 4). The extent of these changes will depend greatly on reservoir capacity relative to amount of water tapped for hydropower production (e.g. Webb & Walling 1997; Hamblin & McAdam 2003; Kvambekk 2012).
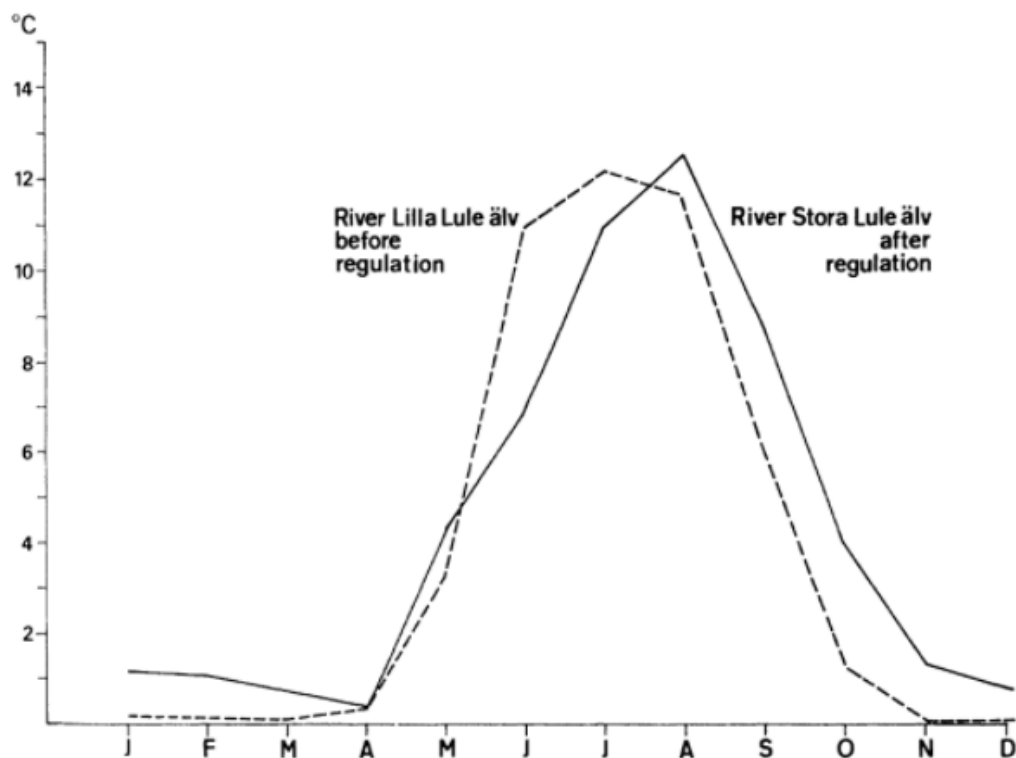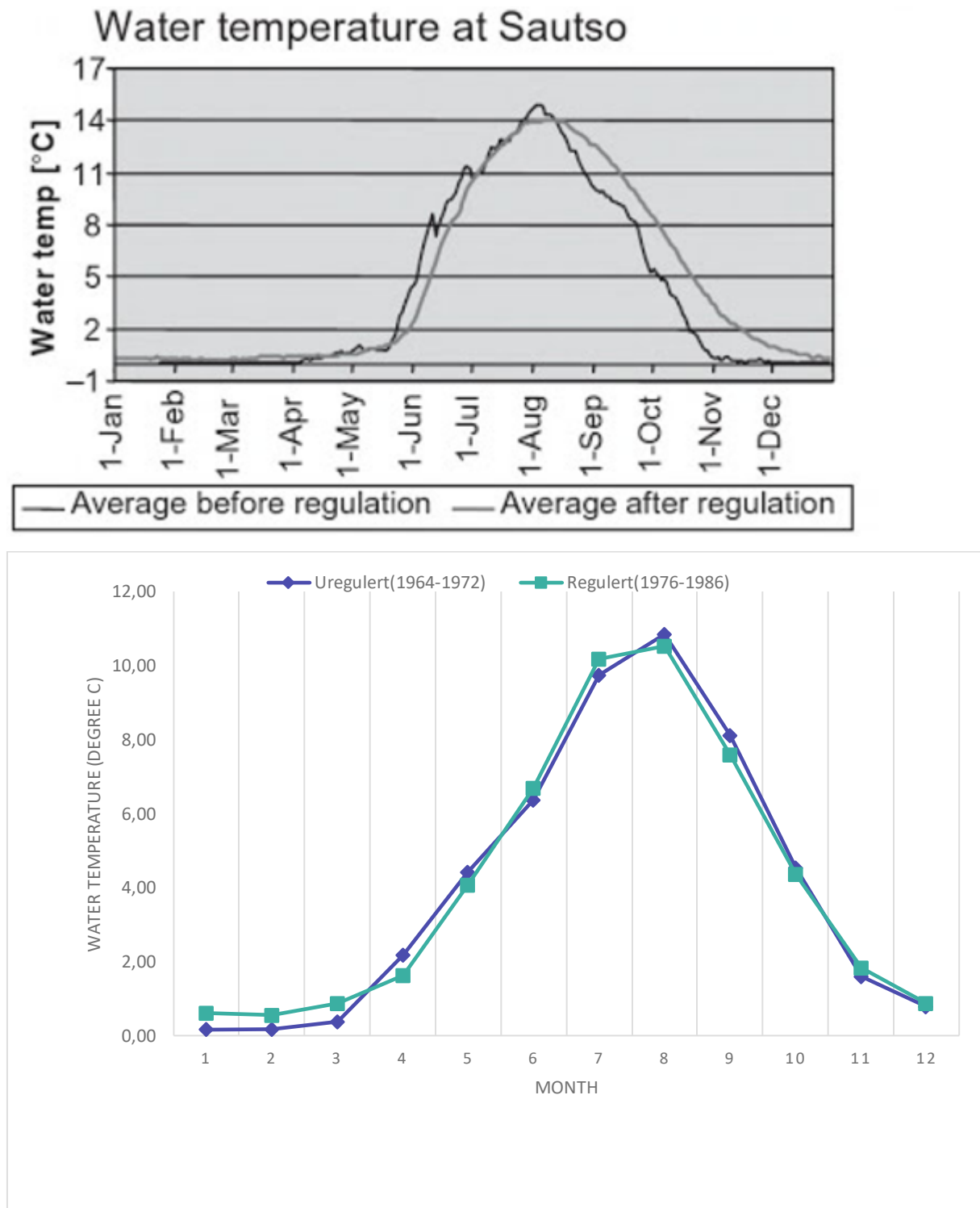
Fig. 4. Top: Monthly mean water temperature in the River Lilla Lule älv before regulation, and after run-of-the-river regulation in River Stora Lule (Müller 1982). Middle: Daily water temperatures at Sautso, Alta River, before and after a moderate high-head river regulation (Thaulow et al. 2009). Bottom: Monthly average temperatures on the Lærdelselva River (at Tønjum) before and after construction of Borgund hydropower plant, which draws water from nine alpine reservoirs.

3.1. Different hydropower regulation systems with different temperature effects

The regulation system and operational strategy are the main drivers behind effected temperature changes. The regulation system can typically be divided into 1) the *high head* system comprising high elevation reservoirs and long transfer tunnels to the power plant (Fig. 5 top, see also Fig. 4) and 2) the *low head* system or run-of-the-river plant (Fig. 5 bottom, see also Fig. 4). A high head system combines relatively low turbine discharges with large head differences, while the low head run of the river plant utilizes a high turbine discharge over a low head. The key to their different effects on water temperatures is water storage capacity and use. With large storage capacity in reservoirs, a high head system may lead to major changes in water temperatures, through typically drawing reservoir water from the hypolimnion water piped directly to the power plant (Fig. 5, 6, 8). This also means bypassing river reaches left with residual or environmental flows, and a seasonal flow redistribution, and thereby temperature, downstream of the power plant outlets. Typically, with no or very little storage capacity and only river reservoirs, low head regulation systems tend to have limited effects on stream water temperatures, but depending on dam/reservoir capacity (Fig. 4, 5). Thus, changes to the seasonal thermal regime of rivers are common in all types of hydropower regulations with storage capacity, allowing redistribution of flow in receiving waters (Asvall 2008; Olden & Naiman 2010a; Dickson, Carrivick & Brown 2012). In broad terms, this leads to reduced magnitude of downstream (1) diurnal and (2) seasonal temperature variation, and (3) winter warming and (4) summer cooling (Poole & Berman 2001; Poff & Zimmerman 2010; Austin *et al.* 2015). Winter warming and summer cooling in particular, may have important ecological effects. However, recent reviews emphasize that the number of studies that quantify the water temperature (and chemistry) effects of dam-induced change on downstream ecological responses, are limited (Haxton & Findlay 2008; Austin *et al.* 2015; Gillespie *et al.* 2015).
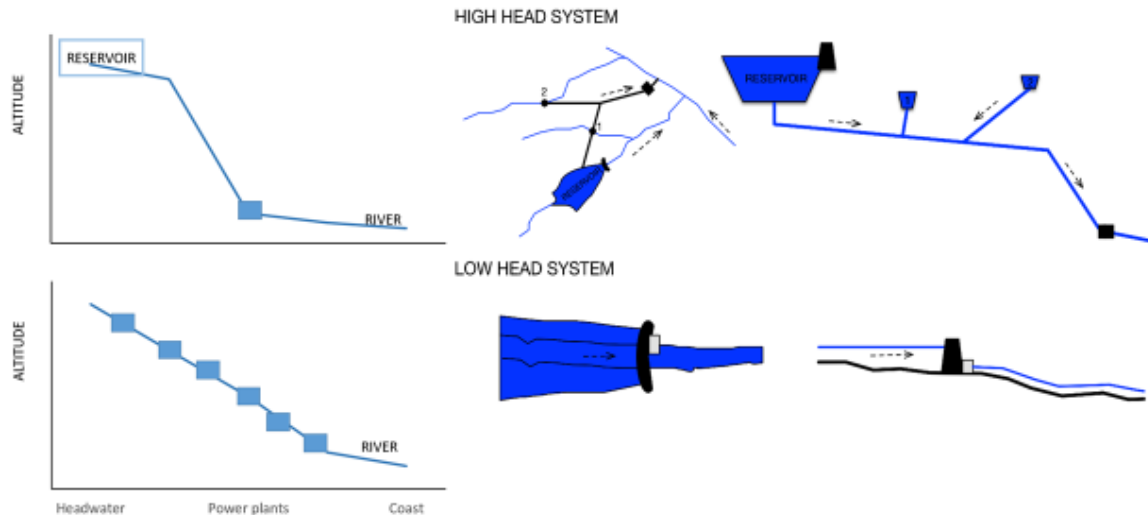
Figure 5.The two typical hydropower regulation systems. Top: a high head system with a high elevation reservoir, tributary intakes, and transfer tunnels to the power plant. Bottom: a low head or run-of-the-river system with intake and power station in the river dam

3.2.   Winter warming

The reservoir temperature gradient ranges from either freezing at the surface in winter, or sun radiation heated water in summer, to around 4°C year round in the deep layers below the thermocline (Fig. 1). Drawing water from an intake in the hypolimnion to the hydropower station will therefore in most cases in winter raise the water temperature in the downstream river reach above the natural seasonal temperature level during winter, from around 0° to >2° (Halleraker *et al.* 2007b; Ugedal *et al.* 2008a) (Fig. 4, 6). There is an additional physical load associated with the temperature increase. It alters downstream ice dynamics, i.e. reduced surface ice and potentially, increased dynamic ice formation (Asvall 2008).
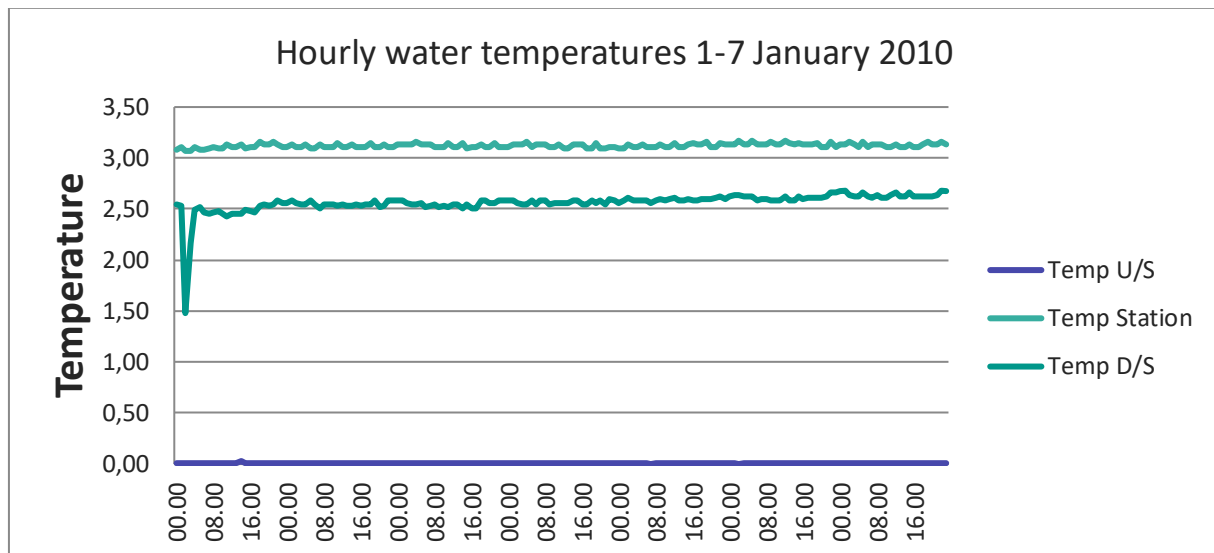
Figure 6. Typical winter water temperature changes effected by hydropower regulation in the River Vallaråi, Norway. Residual flow water with temperature about 0°C (lower blue line, upstream of power station outlet) is mixed with hydropower reservoir water with temperature about 3.2°C (top orange line) from the station outlet, resulting in a downstream temperature of about 2.5°C (middle grey line). The power stations ran continually during the study period.

The bypass reaches with their reduced flow will, however, become more prone to environmental temperatures, and likely experience higher amplitudes during transient fall and spring periods, and more freezing in winter. Spilled water in bypass reaches might trigger ice runs, if the bypasses have an ice cover established during low flow conditions (Timalsina, Becers & Alfredsen 2016).

In the River Alta, North-Norway, a modest temperature rise of 0.3-0.4° C in winter reduced surface ice cover for several km downstream of the power plant (Fig. 4) (Asvall 2008; Ugedal *et al.* 2008a). Halleraker *et al.* (2007b) combined measured and modelled water temperatures from a reservoir to evaluate temperature effects at two stations in the downstream river, resulting from the two alternative mitigation measures dual intakes and altered production regime. The results indicated that the mitigation measures reduced water temperatures in winter within the range 0.1-1°C, and increased temperatures (0.1-2°C) in summer (below), but the potential may be larger, depending on local/regional conditions (Kvambekk 2012).

The potential replacement of the naturally stable mid-winter surface ice period with prolonged transition periods leads to frazil ice formation and correspondingly unstable or no surface ice cover (Ugedal *et al.* 2008a; Timalsina, Charmasson & Alfredsen 2013b; Timalsina, Alfredsen &

Killingtveit 2015a). A prolonged ice formation period will lead to cumulatively increased frazil volume, which may lead to more anchor ice, which can raise water levels and in extreme cases cause local flooding (Stickler *et al.* 2010; Lind & Nilsson 2015) and eventually cause midwinter ice breakups. Warm water releases leading to reduced downstream ice cover may on the other hand reduce the possibility of large ice runs (Gebre *et al.* 2013).

Figure 7. Frazil and anchor ice forming an ice dam causing local flooding in a bypass reach in winter 2017 (From Hjartdøla R., Norway).

3.3. Summer cooling

In summer, the water downstream of the power station is cooled by the contributed hypolimnic water, but to varying degrees, depending on local radiation and residual relative to hydropower flow regimes, and obviously storage capacity (Rolls, Leigh & Sheldon 2012; Finch, Pine & Limburg 2015) (Fig. 4, 8). However, this also gives a potential for adaptive flow regimes, i.e. hydropower flow may be manoeuvered to obtain wanted downstream temperatures. Thermal and seasonal longitudinal effects may be complex (Tvede 1994; Webb & Walling 1997; Webb *et al.* 2008b) largely depending on the balance between residual and regulated flow, but are neither well publicized nor quantified for northern streams (Ellis & Jones 2013) (but see e.g.

(Tvede 1994; Kvambekk 2004) for tentative case studies). For different climatic conditions, i.e. temperate or warmer, and mainly based on larger systems, temperature changes have been shown to persist for many tens of km downstream, and even longer in larger systems (Webb & Walling 1988; Webb & Walling 1993 and references therein; Austin *et al.* 2015)). Such effects obviously depend on reservoir operation, but also local cooling or warming sources downstream of the hydropower outlet, e.g. ground water inflows, tributaries, instream river types, stream gradient, and may remain for 10-40 km or more, downstream (Webb & Walling 1988; Halleraker *et al.* 2007b; Ellis & Jones 2013). The *in situ* factors controlling cooling resp. warming, and the distance needed to cool (in winter) or warm (in summer) water towards the natural water temperature are important to understand, considering the substantial impact zone and physical and ecological effects. Typically, for a glacierised river basin, Tvede (1994) reported a summer temperature increase in a bypass reach, presumably beneficial for biological production, and summer cooling (about 2°C) downstream of the power plant outlet. For rivers with fluctuating production flows, corresponding fluctuating downstream temperature waves (warm resp. cold thermopeaking) exceeding natural daily variation in temperature, may be expected (King 2010; Zolezzi *et al.* 2011), but this is also understudied (Fig. 8).
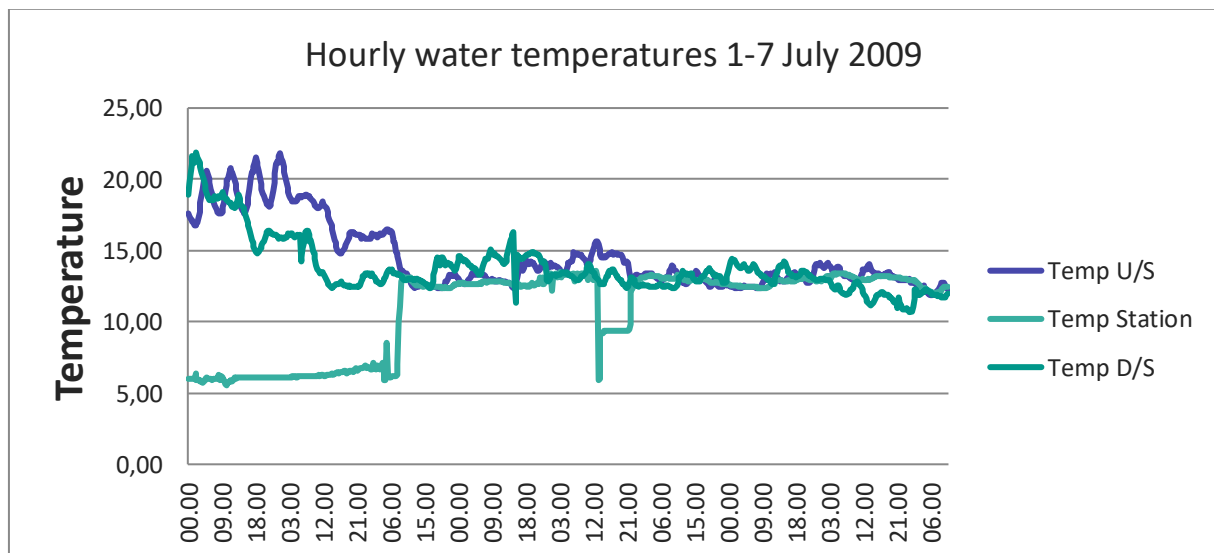
Figure 8. Typical summer water temperature changes effected by hydropower regulation in the River Vallaråi, Norway. Residual flow water (top blue line, upstream of power station outlet) with temperatures around 20°C is mixed with hydropower reservoir water with temperature

about 13°C from the station outlet (lower orange line), resulting in a downstream reduction in temperature by about 5°C (middle grey line), but depending on how the power station is run.

4. BIOLOGICAL IMPACTS AND RESPONSES TO WATER TEMPERATURE CHANGES DUE TO HYDROPOWER REGULATION

Ectothermic native fish and macroinvertebrates are naturally adapted to, but also constrained in production and speed of selection (generation times) by the challenging low-temperature northern (winter) climates (e.g. Ward 1994b; Huryn & Wallace 2000; Elliott & Elliott 2010; Poff & Zimmerman 2010). Biochemical reactions and important physiological responses like metabolism, development and growth are affected by water temperature (Vannote & Sweeney 1980; Elliott & Elliott 2010). Here we consider life-stage dependent and population responses to seasonal temperature variation and to additional hydropower loads, and likely to expected climate change, which are part of their natural thermal strategies (Olsson 1981; Gehrken & Somme 1987; Lillehammer 1987; Lencioni 2004; Danks 2008; Bale & Hayward 2010; Shuter *et al.* 2012; Crozier & Hutchings 2014). The thermal regime in streams may shape important ecological events in fundamental ways (Olden & Naiman 2010b):

- ✓ Accumulation of daily maximum temperatures (above a critical threshold) may be a fundamental variable in shaping the distribution and condition of many aquatic species,
- ✓ Ontogenetic development in freshwater insects and fish respond to the summation of temperature (day-degrees, i.e. the accumulation of daily temperatures above some threshold) as well as absolute temperatures, and
- ✓ fish species and their ontogenetic stages/development have both chronic and acute temperature thresholds for survival, development, growth and reproduction,
- ✓ Thermal cues stimulate fish migration, spawning and egg hatching.

Thus, thermal biology in northern fish species like brown trout and Atlantic salmon influence their life histories from egg and alevin development, via feeding and growth, to spawning migrations, gamete development and spawning (Table 1) (e.g. Solomon & Lightfoot 2008).

Table 1. An overview of thermal biology in the life histories of wild brown trout and Atlantic salmon. (After Solomon & Lightfoot 2008; Elliott & Elliott 2010).

LIFE STAGE	TMEPERATURE EFFECT	BROWN TROUT	ATLANTIC SALMON	NOTE	SELECTED REFERENCES
EGG INCUBATION PERIOD	Determined by day-degrees (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 = $746/(\text{Temp}-0.5323)^{1.2233}$	(Embody 1934; Jungwirth & Winkler 1984; Kane 1988). Formulae from (Jungwirth & Winkler 1984)
EGG SURVIVAL	Depends on temperature.	0 - 13°C Optimum at 8°C?	0 - 16°C Optimum at 6-8°C?	Decrease markedly at higher temperatures. Suboptimal temperatures reduce alevin size, etc. Low interpopulation variability. Some genetical adaptation?	(Gunnes 1979; Reiser & Wesche 1979; Jungwirth & Winkler 1984; Ojanguren, Reyes-Gavilan & Munoz 1999; Ojanguren & Brana 2003; Ornsrud, Gil & Waagbo 2004; Ornsrud *et al.* 2004; Takle, Baeverfjord & Andersen 2004; Takle *et al.* 2006; Syrjanen *et al.* 2008)

ALEVIN DEVELOPMENT, HATCHING TO FIRST FEEDING	Influenced by temperature, similar to eggs.	# of days = $193T^{-0.83}$ $(r^2=0.970)$. At 7.5°C≈ 100 days.	# of days = $472T^{-1.27}$ $(r^2=0.956)$. At 7.5°C≈ 100 days.		(Kane 1988; Jensen, Johnsen & Saksgard 1989; Ojanguren & Brana 2003)
ALEVIN SURVIVAL	Depends on temperature.		< 22°C	Survive higher temperatures than eggs. Lower survival during low temperatures and high flows.	(Jensen & Johnsen 1999; Ojanguren, Reyes-Gavilan & Munoz 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 & Fryer 1995; Elliott & Hurley 1997; Solomon & 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 & Jonsson 1994; Elliott, Hurley & Fryer 1995; Elliott & Hurley 1997; Lobon-Cervia & Rincon 1998; Elliott & Elliott 2010)

		≈ 13°C	≈ 16°C	Interpopulation variation. Genetic adaptation?	Above
MAXIMUM GROWTH					
AVOIDED TEMPERATURES	Cease feeding and growth, induce thermal stress.	<3-4°C and >19-20°C at acclimation 15°C.	?? <6°C and >22°C at acclimation 15°C.	Depends on acclimation, few data for salmon.	(Elliott 1981; Elliott 1994; Elliott & Hurley 1997; Elliott & 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.	(Metcalfe & Thorpe 1990; Saltveit 1990; Jonsson & Labée-Lund 1993)
DEVELOPMENT OF SMOLT	Primarily photoperiod,		Restricted < 3°C, faster		(Staurnes, Sigholt & Gulseth 1994; McCormick *et al.* 1998)

CHARACTERISTICS	influenced by temperature.		with increasing temperature (up to 10°C, and more?)		
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 & Jonsson 1985; Jonsson & Ruud-Hansen 1985; McCormick *et al.* 1998; Byrne *et al.* 2004; Stewart, Middlemas & Youngson 2006; Solomon & 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),		Reduced <≈5°C and >≈16°C, very		(Juanes, Gephard & Beland 2004; Solomon & Sambrook 2004; Saraniemi, Huusko & Tahkola 2008; Quinn, McGinnity & Reed 2016)

	including temperature.	little >20-23°C.		
GAMETE QUALITY	Reduced by high temperatures. ??	>≈18°C	High temperatures reduce egg size, fertility and viability, certain time periods more sensitive.	(King *et al.* 2003; Anderson *et al.* 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 interpopulation variation. Genetic adaptation?	(Webb & McLay 1996; Shields *et al.* 2005; Jonsson & Jonsson 2009)
SPAWNING	Limited temperature range.	1-8°C? <11.5°C		(Webb & McLay 1996; Solomon & Lightfoot 2008)

THERMAL STRESS LIMITS RESTRCTING LONG TERM POPULATION SURVIVAL	High temperatures .	>19.5°C	>22.5°C	Regular occurrence of high temperatures causing thermal stress.	(Solomon & Lightfoot 2008)

4.1.   Winter cold: survival, not production

The common individual winter survival strategy in fish is energy storage (Fig. 9). Additional potential winter strategies are reduced metabolism, tolerance and starvation effected by quiescence (Shuter *et al.* 2012), and shorter behavioral movements or migration to more suitable winter habitat (Rimmer, Paim & Saunders 1984; Saraniemi, Huusko & Tahkola 2008; Linnansaari *et al.* 2009). More activity may result from lack of available refuge habitat, predation risk, easily available food, or perhaps stronger feeding motivation as energy stores are low.
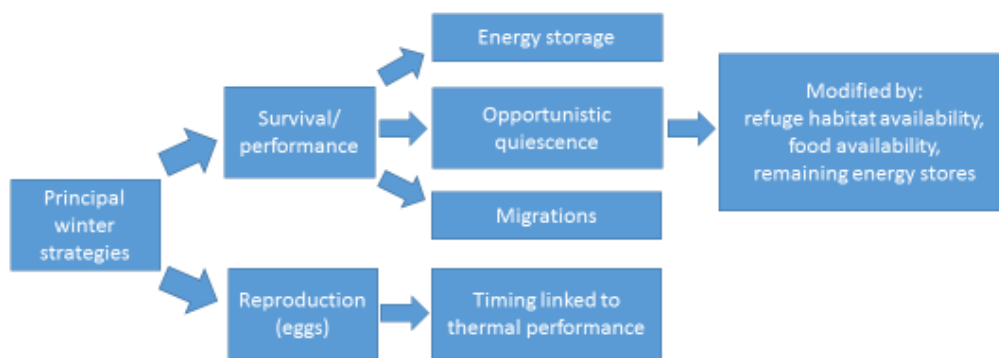
Figure 9. Winter survival strategies in salmon and trout. They store fat in summer and typically adopt a quiescence and starvation strategy during winter cold, and may migrate to more stable deep-slow habitats. A lack of refuge habitat, easily available food and critically low energy reserves may trigger more activity and opportunistic feeding.
They are fall spawners. Spawning time may depend on photoperiod window linked with temperature, and Locally also waterflow, whereas egg development depends on temperature.

Presumably, active feeding under low temperature winter conditions is a dynamic balance between remaining energy reserves and available prey (Fig. 10). If the cost of active feeding is larger than the benefit, the best survival strategy is to adopt quiescence, toleration and starvation. If active feeding is beneficial, then individuals may engage in opportunistic feeding (Metcalfe, Fraser & Burns 1999). For example brown trout may feed year round, but little and with no apparent growth, or even shrinking, in winter (Lien 1978; Elliott 2009; Huusko *et al.* 2011). Furthermore, feeding ability is reduced at typical low winter temperatures and low light levels (Elliott 2011). Mortality may be energy-related and effected through starvation (Finstad

et al. 2004b; Naesje *et al.* 2006). However, mechanistic ice breakup events with their associated physical disturbance effects may also cause very high mortalities, both in eggs and parr (Cunjak, Linnansaari & Caissie 2013). In regulated rivers, mechanistic ice breakup may occur several times and anytime during winter, but to what extent this may cause higher winter mortalities in regulated rivers, largely remains to be documented. Unfortunately, few winter mortality studies are able to separate mortality events during this season. Neither is 'winter' necessarily a critical season for survival (Elliott & Hurley 1998c; Huusko *et al.* 2007). Instead, overwinter survival of juvenile fish appears to be context-dependent, related to specific habitat characteristics, winter duration, and ice regimes of streams (Huusko *et al.* 2007).
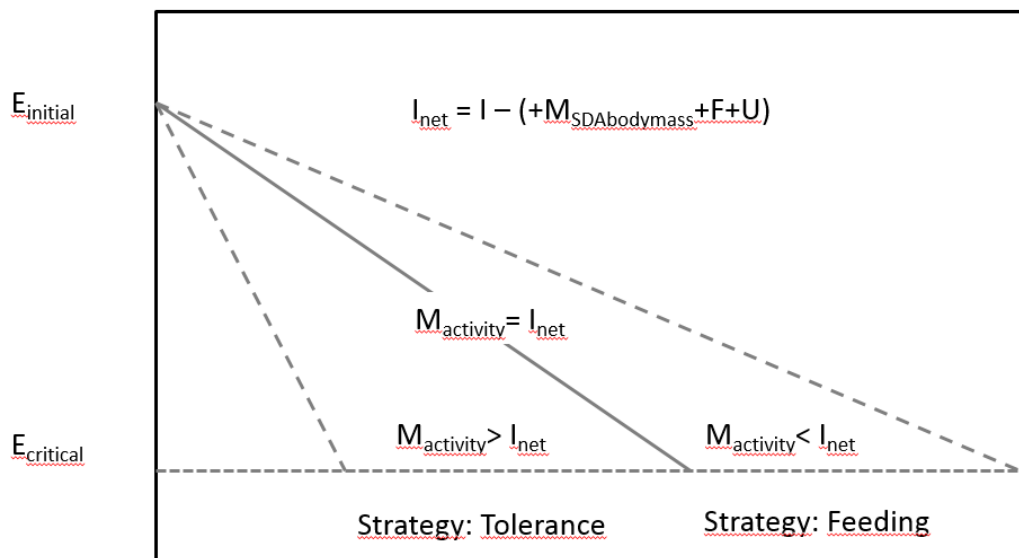
Figure 10. In a biodynamic optimization model under low winter water temperatures, quiescence vs. feeding is controlled by: 1) the pre-winter level of stored energy ($E_{initial}$), 2) the critical limit for survival (E_{cri}), in relation to 3) the ingestion rate (I), minus the energetic cost associated with that feeding ($M_{activity}$, $M_{SDAbodymass}$, F_{aeces}, U_{rea}), and 4) the obligate energy demand ($M_{basal} + M_{ParasiteLoad}$). (From Shuter et al. 2012).

4.1.1. Low temperature fish behaviors

Since foraging during low temperatures in winter is rare for salmon and trout, behaviors in winter may primarily serve survival, by reducing activity energy expenditure (above), but also

risk. Bioenergetic optimization models are modified by risk (Reinhardt & Healey 1999) in the form of predation (Valdimarsson & Metcalfe 1998), but probably also ice formation (one behavior serves both). It likely explains why salmon and trout become nocturnal and more shelter-seeking at low temperatures (Fraser, Metcalfe & Thorpe 1993; Heggenes *et al.* 1993; Linnansaari, Cunjak & Newbury 2008; Watz *et al.* 2014), and independent of season (Fraser *et al.* 1995). As temperatures drop in the fall to 6-8°C or lower, salmon and trout typically become less active, seek shelter more in the substratum or deep areas, and become more nocturnal (Rimmer, Paim & Saunders 1984; Cunjak, Power & Barton 1986; Heggenes *et al.* 1993). However, like winter quiescence, nocturnalism may be modified by individual state and feeding motivation (Metcalfe, Fraser & Burns 1998; Valdimarsson & Metcalfe 1999). Salmon and trout also become less aggressive and less efficient foragers at lower light levels and temperatures (Valdimarsson & Metcalfe 2001; Elliott 2011), and may therefore become more aggregated in smaller more suitable deep-slow winter habitat areas (Cunjak, Prowse & Parrish 1998; Griffiths, Armstrong & Metcalfe 2003). Such low-velocity microhabitats reduce swimming activity cost, and may reduce predation risk (Valdimarsson, Metcalfe & Skulason 2000). Therefore, cover and shelter microhabitats become more important at the onset of winter. In streams in winter the heat loss and frazil and anchor ice formation is also greatest at night, when salmon and trout preferably are active. However, in spite of a number of winter studies, salmon or trout trapped in ice have to our knowledge, not been reported (see Heggenes *et al.* 2016 for a detailed report on fish and ice phenomena), and salmonids appear to cope well with the more regular ice phenomena. For macroinvertebrates, however, ice encasing occur (below).

This low temperature shelter-nocturnalism salmon and trout behavior remains throughout the winter, and often implies limited *in situ* movements (≤10m) (Stickler *et al.* 2008a; Linnansaari & Cunjak 2013; Kemp *et al.* 2017). Therefore, for fish facing changed winter conditions due to hydropower regulation, *in situ* high or increased embeddedness (reduced substrate shelter), e.g. due to increased sedimentation, will negatively influence winter habitat quality. Lack of shelter increase initial mass loss rates substantially (Finstad *et al.* 2007; Koljonen *et al.* 2012) and juveniles may move to areas providing more shelter (Linnansaari, Cunjak & Newbury 2008; Linnansaari *et al.* 2009), thus also increasing energy cost. Availability of shelter may override other environmental factors like flow.

4.1.2. Macroinvertebrate winter production and ice

Most studies of benthic macronvertebrate production emphasize the effect of abiotic factors on production, i.e. temperature, habitat, water chemistry (Huryn & Wallace 2000). Like for fish, seasonally low temperatures (and food limitation) clearly constrain macroinvertebrate production, which is lowest in cool-temperate and arctic streams (Huryn & Wallace 2000). There are several strategies to cope with and even take advantage of winter conditions. During summer benthic and periphytic algae are a major food source for grazing macroinvertebrates, while during winter allochthonous organic plant material (leaf litter) provides a major food source that is utilized by winter growing shredder species (Brittain 1983; Lillehammer *et al.* 1989; Haapala & Muotka 1998). Other species undergo quiescence or diapause, most commonly in the egg stage, in order to avoid unfavourable periods (Brittain 1990). Likewise, other species avoid unfavourable periods in winter by entering into more cold tolerant quiescence or diapause (Harper & Hynes 1970; Lencioni 2004; Danks 2008), usually cued by photoperiod. Another freeze avoiding strategy, which can be coupled with diapause/quiescence, is to move, i.e. behavioural avoidance (Bale & Hayward 2010). Insects may move down into the substrate, even into the hyporheic, especially in groundwater-fed areas (Lencioni 2004). A further strategy is to undertake seasonal movements into tributaries or deeper waters (Olsson 1983). Alternatively, certain species, notably within the Diptera, but also in Plecoptera, display freezing tolerance and a stay-put strategy (Lillehammer 1987; Lencioni 2004). This may also involve seasonal changes in cold tolerance underpinned by a complex of interacting processes (e.g. ice nucleating agents, cryoprotectants, antifreeze proteins, changes in membrane lipid composition) (Bale & Hayward 2010). Although most species can invoke one or more of these strategies to tolerate thermally stressful environments, the majority of insects die from the effects of cold water rather than freezing (Bale & Hayward 2010).

Modified water temperatures, e.g. by hydropower regulation (above), may have major effects on normal rates of development and life cycles, and even lead to extinction of specialist species, as the many facets of growth and emergence are affected and even cued by water temperature (Brittain 1982; Raddum 1985; Lillehammer *et al.* 1989). Moreover, since photoperiod is the dominant diapause-inducing cue and unaffected by hydropower regulation, a modified temperature regime may lead to de-coupling of synchrony between diapause-sensitive life

stages and thermally challenging environments. The species that have a rigid synchronous one year or unoivoltine life cycles are most at risk, while species with flexible life cycle length will be favored (Brittain 1991). Species with long life cycles, especially among Plecoptera, are adversely affected by regulation (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). In the Norwegian River Surna, located in an oceanic region with low invertebrate richness, coldwater discharge from the power station during summer caused few changes in the species composition of Ephemeroptera, Plecoptera and Trichoptera as these were widely distributed eurythermal species. However, within the Chironomidae there was a major shift to cold stenothermal species (Saltveit, Bremnes & Brittain 1994). In contrast, in more continental regions with a high species richness, there are usually major changes in all orders as a result of cooler waters, especially among the Plecoptera (Saltveit, Brittain & Lillehammer 1987). In winter, negative impacts from hydropower regulation may occur if it leads to release of warmer reservoir water downstream of power plants (Raddum 1985), leading to reduced snow and ice cover which may expose macroinvertebrates to more severe air temperatures, and increased frequency of freeze-thaw cycles may increase risks of ice encasement (Bale & Hayward 2010). However, benthic organisms appear to survive entrapment in anchor ice (Brown, Clothier & Alvord 1953; Benson 1955; Oswood, Miller & Irons 1991). Nevertheless, mechanical disruption of the substrate may dislodge benthic invertebrates (Butler & Hawthorne 1979) and lead to increased downstream drift (Finni & Chandler 1979) and even faunal depletion in some cases (Colbo 1979), although not in others (Brown, Clothier & Alvord 1953).

Severe winters have been shown to reduce, at least in the short term, both benthic abundance and taxonomic richness (Hoffsten 2003). In laboratory experiments, several benthic species survived exposure to sub-zero temperatures when supercooled, but succumbed when chilled in contact with ice (Frisbie & Lee 1997). Larvae of Chironomidae and Empidae often display high survival rates when thawed out of frozen stream gravels (Irons III, Miller & Oswood 1993; Lencioni 2004). However, other taxa, including Gastropoda, Hirudinea and a few Trichoptera, also appear to survive freezing in stream gravels (Olsson 1981). 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, Miller & Irons 1991). Water content

is a critical factor in determining cold-hardiness and eggs of the plecopteran, *Arcynopteryx compacta,* that overwinter in alpine streams, increase their cold-hardiness by dehydration (Gehrken & Somme 1987). At the onset of winter, they enter a period of diapause, and when subject to freezing diapause is broken earlier than when not frozen (Lillehammer 1987) (Lillehammer 1987).

Although most aquatic insects emerge during the ice-free period, some species emerge during winter. Emergence and mating beneath ice cover or through cracks in the ice cover/snow pack has been observed in Chironomidae, Trichoptera and Plecoptera (Hågvar & Østbye 1973; Lencioni 2004).

Frazil ice events may increase post-event drift (Martin *et al.* 2001; Sertic Peric & Robinson 2015), but also make benthic animals less available as anchor ice may form vast blankets of ice on the river bed. Invertebrate abundance may be reduced throughout winter (Clifford 1972; Martin *et al.* 2001), because of reduced water flow (Waringer 1992), reduced invertebrate activity (Martin *et al.* 2001; Ferreira & Canhoto 2014), and perhaps increased food availability in the hyporheic zone, resulting from increased input of allochtonous organic material in the autumn (Hildebrand 1974; Vannote *et al.* 1980; Haapala & Muotka 1998; Dekar, Magoulick & Huxel 2009). Drift may often be light dependent with higher drift at dusk and night than during day (Elliott 1965; Brittain & Eikeland 1988; Neale *et al.* 2008; Oberrisser & Waringer 2011). However, this periodicity appears plastic and may break down during continuous summer light at northern latitudes (Brittain & Eikeland 1988), or depend on other *in situ* environmental factors, e.g. be absent in high altitude snow and glacier fed streams (Hieber, Robinson & Uehlinger 2003), and/or in winter (Hieber, Robinson & Uehlinger 2003; Johansen *et al.* 2010).

4.1.3.   Low temperatures, low performance

Reduced detection and capture efficiencies at low light levels (Fraser & Metcalfe 1997; Valdimarsson & Metcalfe 2001) as well as at low temperatures (Elliott 2011; Watz *et al.* 2014), combined with reduced drift/low feeding resource biomass during the winter season (Brittain & Eikeland 1988; Matthaei, Werthmuller & Frutiger 1998; Martin *et al.* 2001), make active drift feeding in winter less profitable (Fig. 11). Swimming ability is also substantially reduced at low temperatures (Fig. 12). However, opportunistic feeding may remain, in particular during more

benign winter conditions (Fig. 11) (Metcalfe, Fraser & Burns 1999; Lagarrigue *et al.* 2002; Kemp *et al.* 2017). In more high gradients habitats, e.g. riffles providing important substrate shelter and possibly increased availability of benthic food in winter (Kreivi *et al.* 1999; Mitro & Zale 2002), benthic feeding may be relatively more profitable in winter than drift feeding, due to the lower cost by not holding station in the current (Fig. 11). Such habitats may represent important winter refuges for smaller fish (Huusko *et al.* 2007; Stickler *et al.* 2008b).

Higher benthic macroinvertebrate abundance in winter may result from increased input of allocthonous material in the fall, in particular in smaller, natural streams (Haapala, Muotka & Markkola 2001). However, results are ambiguous, and winter reductions are also reported (Morin, Rodriguez & Nadon 1995; Martin *et al.* 2001). Flow and season may be confounded in invertebrate field studies, which generally depend on ice-free streams (Suren & Jowett 2006; Leung, Rosenfeld & Bernhardt 2009). Supercooled water will reduce macroinvertebrate abundance (Martin *et al.* 2001; Hoffsten 2003). Increased downstream temperatures in the regulated Aurland River during winter increased growth rates in the mayfly, *Baetis rhodani* (Raddum & Fjellheim 1993a) Macroinvertebrate growth and development is temperature dependent (Vannote & Sweeney 1980; Huryn & Wallace 2000), but continues in many species even at low winter temperatures, as found in extreme Arctic environments (e.g. Coulson *et al.* 2014). Potentially higher invertebrate production in winter-warmer regulated rivers may precipitate more opportunistic feeding, but not necessarily benefit fish growth. Moreover, it likely gives an earlier start of the growth season. However, such beneficial effects are likely confounded by simultaneous changes in flow regime and summer temperatures (Cereghino, Cugny & Lavandier 2002; Jackson, Gibbins & Soulsby 2007; Bruno *et al.* 2009; Bruno *et al.* 2013; Miller & Judson 2014).
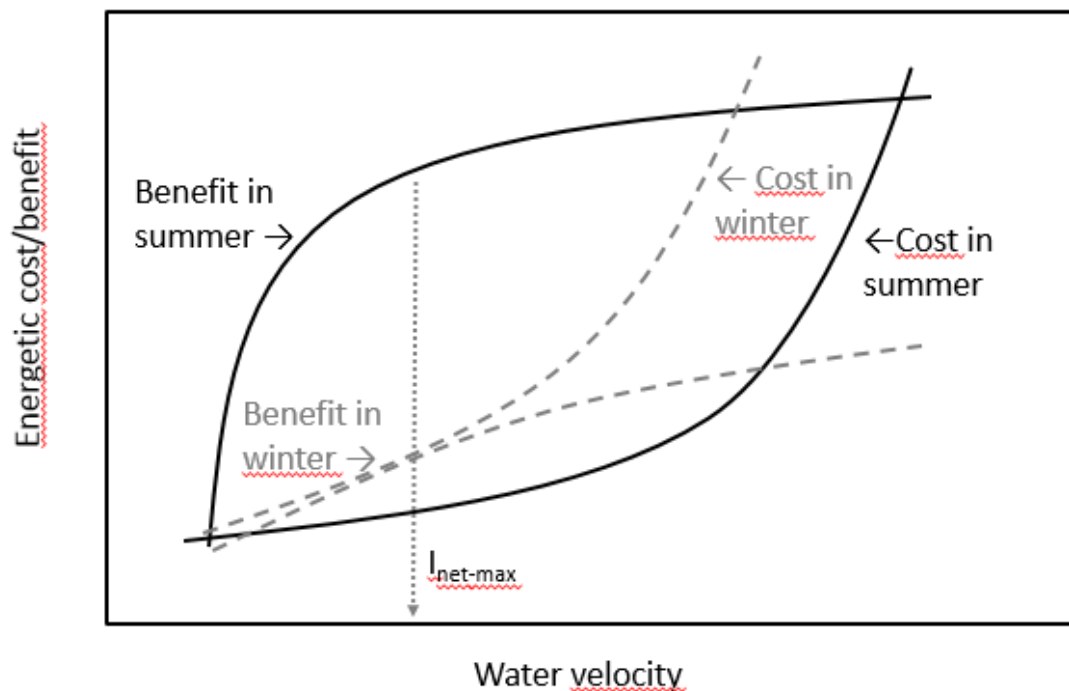
Figure 11. A conceptual cost-benefit model for drift-feeding salmonids in habitats with low perceived predation risk, in summer (solid lines) and in winter (darted lines). Dotted line represent maximum net energy gain. In winter, reduced drift availability and capture success and increased cost will reduce or eliminate the net energy gain potential (dotted curves). The relative benefit from benthic feeding may increase in winter.
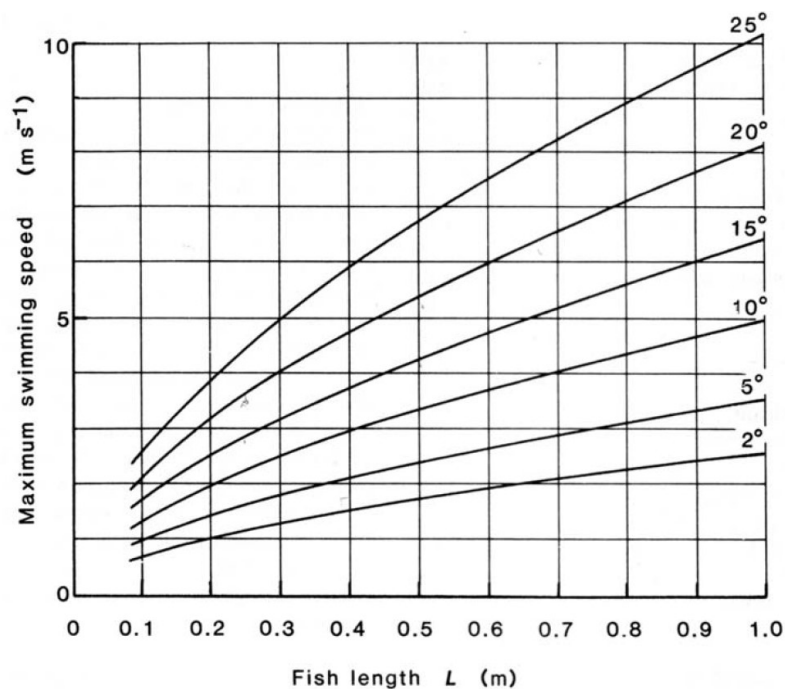
Figure 12. Theoretical maximum swimming (burst) speeds for salmonids at different temperatures. (After Beach 1984; From Solomon & Lightfoot 2008)

In the Alta River, reduced ice cover in the reach below the dam caused by higher winter water temperatures led to an initial increase in algal biomass, although algal biomass declined over the ensuring years along with reduced benthic densities (Koksvik & Reinertsen 2008). However, benthic invertebrate biomass changed little as the density reduction was mostly among the small organisms, primarily Chironomidae.

Feeding and growth in northern populations, at least for fish, appear to some extent to be adapted to the longer and more intense winters. Northern salmon populations tend to grow better under the ice in the dark than their southern cousins (Finstad *et al.* 2004a). They in turn, grow better in the light without surface ice (Finstad & Forseth 2006). The pattern is similar for food consumption (Finstad & Forseth 2006). Trout appear to grow better than expected in colder rivers (Jensen, Forseth & Johnsen 2000), suggesting adaptations.

4.1.4. Temperature adaptations

Within macroinvertebrates, there are species which show considerable morphological and ecological variation, permitting adaptation to a wide range of environments, notably widespread species with flexible life cycle length (Brittain & Saltveit 1989; Brittain 1991; Raddum & Fjellheim 1993b). The high species richness among aquatic macroinvertebrates also allows for species specific adaptation to local environmental conditions (Lillehammer *et al.* 1989), although species with narrow environmental limits or particular environmental cues risk becoming extinct when conditions change (Lehmkuhl 1972).

In species like salmon and trout with a wide geographic distribution, and constraints on gene flow imposed by watershed isolation and restricted spatial dimensionality, intra-specific variation together with local adaptation in winter strategies, may be expected. Indeed, differences both in warm and cold water thermal performance exist among salmon and trout populations (Forseth *et al.* 2009; Anttila *et al.* 2013; Hartman & Porto 2014). Intraspecific phenotypic plasticity is important (below). There is, however, limited indication of local thermal adaptation (Jensen *et al.* 2008; Skoglund *et al.* 2011; Finstad & Jonsson 2012; Meier *et al.* 2014). In some cases there appears to be some genetically based local adaptation to winter climates,

notably energy storage (Alvarez, Cano & Nicieza 2006; Finstad *et al.* 2010; Berg *et al.* 2011; Crespel *et al.* 2013).

Thermal adaptation in ectotherms may come as 1) thermal adaptation to local optima, or as 2) countergradient adaptation, meaning that populations from hostile environments, e.g. severe winter climates, may perform better at all temperatures than populations from benign environments (Forseth *et al.* 2009; Elliott & Elliott 2010). There is, however, not much support for a thermal optima adaptation hypothesis in different (juvenile) coldwater brown trout and Atlantic salmon populations. Trout and salmon (maximum) growth capacity may vary among populations, but did neither correlate with local natural temperature optima, nor indicate counter gradient variation in growth (Jonsson *et al.* 2001; Larsson & Berglund 2006; Forseth *et al.* 2009; Baerum *et al.* 2016). Instead, adaptive variation in growth potential may be related to factors affecting reproductive success (Forseth *et al.* 2009; Jonsson & Jonsson 2009; Elliott & Elliott 2010). However, some studies in brown trout suggest that some form of local counter gradient adaptation may exist (Jensen, Forseth & Johnsen 2000; Finstad, Naesje & Forseth 2004; Nicola & Almodovar 2004; Alvarez, Cano & Nicieza 2006). To the limited extent that thermal adaptations have been suggested, counter gradient adaptations in (very) cold environments appear important (Jensen, Forseth & Johnsen 2000; Finstad, Naesje & Forseth 2004; Nicola & Almodovar 2004; Elliott & Elliott 2010). The apparent lack of local thermal adaptations in Atlantic salmon have 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 sedentary brown trout, different population-specific thermal regimes throughout its life history is more likely, in particular in colder streams, as some studies have indicated (Jensen, Forseth & Johnsen 2000; Nicola & Almodovar 2004; Alvarez, Cano & Nicieza 2006), although environmental variability may account for most of the observed variation in annual growth rates. It is important to note that acclimation regimes may result in different (intermittent) thermal tolerances and/or optima (Konecki, Woody & Quinn 1995). The negligible evidence of intraspecific adaptation for temperature optima may be surprising, but adaptation of enzyme systems to different temperatures appears to come at a high cost (Portner 2006; Shuter *et al.* 2012).

4.2.   Summer warming: growth

Water temperature and available food supply, are the most important environmental factors influencing the growth of salmon and trout in streams, provided other biotic and abiotic factors are within tolerable limits (Tab. 2) (Forseth, Letcher & Johansen 2010; Logez & Pont 2011; Budy *et al.* 2013). Summer is the principal feeding and growing season for fish and invertebrates, primarily for temperature reasons.

4.2.1.   Temperature tolerances

Tolerance and changes in the performance of fish like salmon and trout with temperature is extensively researched (Fry 1971; Elliott 1994; Larsson & Berglund 2006).

Table 2. Temperature tolerances (°C) for survival of Atlantic salmon and brown trout. (After Elliott & Elliott 2010).

Life stage	Atlantic salmon		Brown trout	
	Lower	*Upper*	*Lower*	*Upper*
Eggs	0	16	0	13
Alevins				
Long term*	0-2	23-24	0-1	20-22
Short term**	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

*Incipient Lethal Temperature (ILT): tolerance for a long time period, usually 7 days.**Ultimate Lethal Temperature (ULT): tolerance for a short time period, usually 10 min.

Intraspecific variation in thermal tolerance may be substantial, depending on developmental stage and individual (Tab. 2, 3). The small young-of-the-year, in particular the alevins (young with yolk sac) hatching with increasing temperatures in spring, are less tolerant to thermal stress (Elliott & Elliott 2010; Breau, Cunjak & Peake 2011; Ayllon *et al.* 2013), and eggs have the lowest tolerance (Elliott & Elliott 2010) (Tab. 3). Atlantic salmon tolerate the higher temperature range. The lower limit is close to zero for both species, but salmon has the poorer tolerance to near-zero temperatures (Table 2). This is reflected in a more limited northern distribution and absence from some glacier-fed rivers, e.g. in Norway. These temperature tolerances remain similar over a wide geographical range with negligible indications of regional adaptations (Elliott & Elliott 2010).

4.2.2.   Temperature preferences

Salmonid species appear to be physiologically adapted for optimal performance within a specific range of summer temperatures (Table 1, 2, 3) (Clarke & Portner 2010; Shuter *et al.* 2012). Growth may stop according to lower and upper thermal limits. The ecologically relevant thermal window (ERTW) is bounded by the upper and lower temperatures across which the aerobic scope (the difference between the highest and lowest rates of aerobic respiration) is high and relatively constant (Shuter *et al.* 2012). The definition 'species-specific preferred temperature' ±2°C seems to work quite well (Magnuson, Crowder & Medvick 1979)(although the optimal growth and preferred temperature may be shifted towards 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). Obviously, species with lower preferred temperatures are likely to be more efficient foragers during low-temperatures. Interestingly, most freshwater fish, including the coldwater salmon and trout, have preferred temperatures well above 4-5°C (Table 1, 2, 3) (Elliott & Elliott 2010; Shuter *et al.* 2012), whereas ambient winter temperatures are well below that. Thus, winter is about survival in salmon and trout, effected through energy storage and winter toleration and starvation.

4.2.3.   Temperature dependent growth

Performance limits, expressed as feeding and growth, vary more (Table 3) with substantial individual and population differences primarily due to phenotypic plasticity. It is important to note that the optimum growth temperature will decrease with decreasing energy intake (Elliott & Elliott 2010). Values in Table 3 are for maximum rations in the laboratory. Therefore, optimum will tend to be lower in nature.

Table 3. Temperature limits (°C) for growth range, optimum growth (on maximum rations), and maximum growth efficiency for Atlantic salmon and brown trout. (After Elliott & Elliott 2010).

Species	Lower	Upper	Optimum	Growth efficiency
Atlantic salmon				
U.K.	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	

For relatively benign environmental conditions, maximum ration (laboratory) growth models for salmonids may be good approximations of growth in natural streams, and demonstrate the importance of temperature, for example for brown trout (Fig. 13)(Elliott 2009; Elliott & Elliott 2010):

$$W_t = [W^b_0 + bc(T-T_{LIM})t/\{100(T_m-T_{LIM})\}]^{1/b}$$

where W_0 is the initial fish mass,

W_t is the final fish mass after t days at T °C and

$T_{LIM} = T_L$ if $T \leq T_M$ or $T_{LIM} = T_U$ if $T > T_M$.

The temperature for optimum growth is T_M (see Table 3), and T_L and T_U are the lower and upper temperatures at which growth rate is zero, the mass exponent b is the power transformation of mass that produces linear growth with time, c is the growth rate of a 1 g fish at the optimum temperature range 3.8 – 21.7 °C, and may be estimated as $b = 0.308$, $c = 2.803$, $T_M = 13.11$, $T_L = 3.56$ and $T_U = 19.48$ (Fig. 13)(Elliott, Hurley & Fryer 1995; Elliott 2009; Elliott & Elliott 2010). Importantly, if during the summer growth season, feeding and growth is hampered for some reason, for example by limited habitat during low flows and droughts in summer, trout is able of compensatory growth (Elliott 2009; Elliott 2015). Corresponding growth models exist for juvenile salmon (Fig. 13) (Elliott & Hurley 1997; Forseth *et al.* 2001; Jonsson *et al.* 2001). Such growth models are robust to assumed base growth temperatures (Chezik, Lester & Venturelli 2014) and versatile tools that may be used in comparative studies, e.g. to control for influence of other environmental factors, as food availability (Sanchez-Hernandez *et al.* 2016) or hydropower regulation.
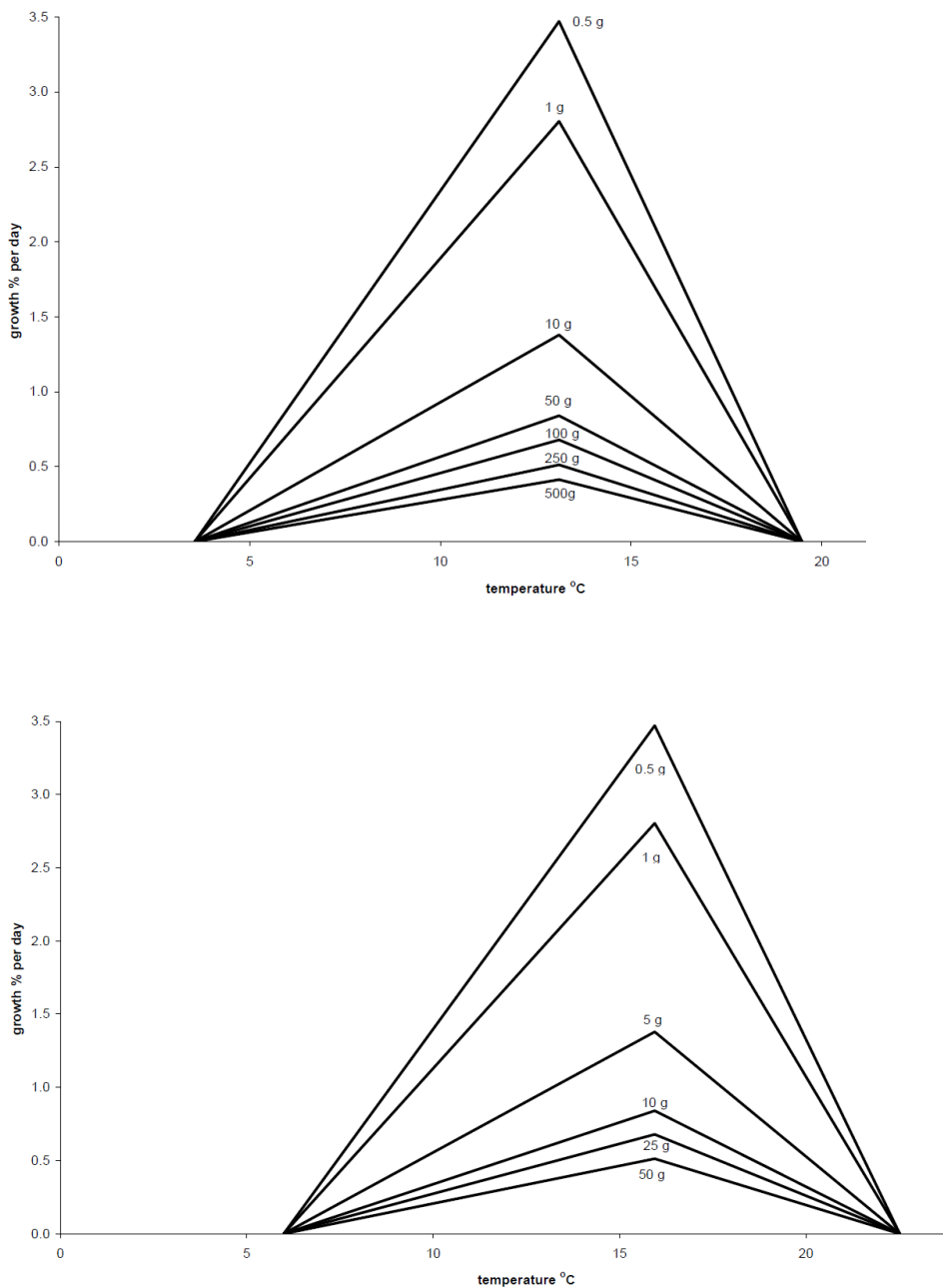
Figure 13. Relationship between temperature and predicted growth (in per cent of body weight per day) for brown trout (top) and Atlantic salmon (bottom) at various sizes (weight in g) fed maximum rations. (From Solomon & Lightfoot 2008).

The duration of the warm versus the cold season will directly affect fish growth and production in a cold stream. Build-up of larger fat reserves in summer and lower depletion rates in winter, may to some extent compensate for longer winters (e. g. Shuter *et al.* 2012). Indeed, juvenile northern salmon populations show lower lipid-depletion rates during winter than southern

populations, and storage lipid levels cluster close to critical limits for survival (Finstad *et al.* 2010). Thus, salmon and trout from northern populations have larger pre-winter lipid stores (Berg *et al.* 2009; Berg *et al.* 2011), although there is variation among local rivers, and show a stronger positive scaling of feeding activity with decreasing energy levels, i.e. presumably compensatory adaptive differences in state dependent feeding motivation (Finstad *et al.* 2010). This may explain the observed variation in lower temperature for feeding activity in salmon and trout (Table 3).

In most aquatic macroinvertebrates, the length of the egg development period is governed by water temperature (e.g. Lillehammer *et al.* 1989; Gillooly & Dodson 2000; Elliott & Humpesch 2010), mostly expressed by the formula

$$Y = aT^{-b}$$

where Y = no of days,

T = temperature,

and a and b are constants.

However, the degree of temperature dependence varies from species to species. For example, egg development is more temperature dependent in Ephemeroptera compared to Plecoptera and the number of degree days required for egg development is generally greater in Ephemeroptera compared to Plecoptera (Brittain 1990). Growth of nymphs and larvae is also temperature dependent in most species (e.g. Elliott 1984), although a few plecopteran species have been shown to grow at similar rates over a wide temperature range (Brittain, Lillehammer & Saltveit 1986). Optimal temperatures for growth vary widely among aquatic insects and it has been hypothesised that, in hemimetabolous aquatic insects adult body size and fecundity depend largely on thermal conditions during development (Sweeney & Vannote 1978; Vannote & Sweeney 1980) and that smaller adults and reduced fecundity result from suboptimal temperatures. Thus, the geographical distribution of individual species is limited by ever-increasing divergence from optimal water temperatures and ensuing reduced fecundity. When the growing season is reduced, some insects may develop cold hardiness without entering diapause, maintain a slow but continuous growth (Lencioni 2004).

4.2.4. Temperature and water flow interactions

River flow influence key factors like temperature (and other factors, see e.g. Armstrong & Nislow 2012; Warren, Dunbar & Smith 2015) (for a more detailed discussion see Heggenes *et al.* 2016). In general it remains difficult to isolate the contributions of water temperature and water flow to biotic responses (Olden & Naiman 2010b).

Temperature-flow interactions may have different effects on the different life stages of fish like salmon and trout (Table 1), with early ontogeny being particularly sensitive (e.g. Young, Cech & Thompson 2011; Nislow & Armstrong 2012; Warren, Dunbar & Smith 2015). In regulated streams other important interacting factors are channel morphology, substrate type, critical flow, before-conditions, timing (day/night, season), magnitude, duration, frequency, rate of change, and if in a hydro-peaked system also down-ramping rate, ramping amplitude, frequency of flow fluctuations, prior flow conditions, timing of pulse (see Young, Cech & Thompson 2011; Rolls, Leigh & Sheldon 2012 for reviews).

Diverted or increased flows, for example by hydropower production, will change the longitudinal temperature regimes. Reduced flows will depend more on local environmental conditions, but more on flow manipulations for increased flows. Reduced summer flows, e.g. in bypass reaches, may exacerbate temperature stress and hypoxic effects (Elliott 2000; Milner *et al.* 2003). Winter low flows may lead to increased ice formation, reduced available habitat and associated risk of fish stress and kills (Borgstrom 2001; Huusko *et al.* 2007; Cunjak, Linnansaari & Caissie 2013).

Refugia habitat during low flows obviously includes deeper water (Huntingford *et al.* 1999; Elliott 2000; Armstrong *et al.* 2003; Davey & Kelly 2007; Conallin *et al.* 2014). It may also include deep or more shallow thermal refugia (pool, side channel, tributary) (Brown 1999; Baird & Krueger 2003; Breau, Cunjak & Bremset 2007; Stevens & DuPont 2011) and the hyporheic zone (Boxall, Giannico & Li 2008; Heggenes, Bremset & Brabrand 2013). These refugia are often associated with more temperature-stable groundwater inflow both in summer (lower temperatures) (Baird & Krueger 2003; Breau, Cunjak & Bremset 2007; Boxall, Giannico & Li 2008) and winter (higher ice-free temperatures) (Brown 1999).

Low flows, e.g. during summer (Elliott, Hurley & Elliott 1997; Bell, Elliott & Moore 2000; Hvidsten *et al.* 2015) or in recruitment streams in winter, may reduce salmonid production (Elliott, Hurley & Elliott 1997; Borgstrom 2001; Elliott 2006; Cunjak, Linnansaari & Caissie 2013;

Hvidsten *et al.* 2015). Low flows leading to dry conditions will increase mortality of fish eggs deposited in the substratum the previous fall. However, presence of groundwater influx may increase survival significantly (Casas-Mulet *et al.* 2015; Casas-Mulet, Saltveit & Alfredsen 2015). For insects, low winter flows below a water transfer dam on the Norwegian River Glomma led to a severe reduction in the winter generation of the bivoltine mayfly *Baetis rhodani*, while the filter-feeding Trichoptera increased in densities (Brittain, Lillehammer & Bildeng 1984). One of the dominant trichopteran species, *Arctopsyche ladogensis*, had a mixture of one and two-year life cycles, enabling it to adapt to the changed temperature and flow regime (Brittain & Bildeng 1995).

Restored/increased flows in regulated rivers have resulted in higher salmonid production (Sabaton *et al.* 2008). Higher minimum discharge in winter after regulation, and associated higher water temperatures in parts of the longitudinal profile, may improve parr survival rates and subsequent smolt production (Hvidsten *et al.* 2015). It is, however, not easy to tease apart flow and temperature effects.

High flows may initially increase available habitat and benefit egg and juvenile winter fish survival in streams (Frenette *et al.* 1984; Cunjak, Linnansaari & Caissie 2013; Hvidsten *et al.* 2015). The relatively short emergence and alevin phase is primarily regulated by temperature (Elliott & Hurley 1998a; Elliott 2009; Cunjak, Linnansaari & Caissie 2013). Alevins and young larvae have limited swimming capacity and drift downstream for dispersal, which confers energetic benefits (Einum *et al.* 2011). The cost is, however, vulnerability to downstream displacement and 'washout' during high flows (Heggenes & Traaen 1988; Crisp & Hurley 1991; Fausch *et al.* 2001; Pavlov *et al.* 2008; Wolter & Sukhodolov 2008) and washed out larvae may be moribound (Elliott 1994). The ability to swim and maintain position by seeking out low-velocity micro-niches (Heggenes, Bagliniere & Cunjak 1999; Heggenes 2002; Armstrong *et al.* 2003) improves rapidly with increasing temperature (above) and body size (Heggenes 1988). Effects of regulation-induced temperature changes/increases in early spring is limited or lacking, and thus need research and competence development.

Hydro-peaked systems tend to aggravate high-low flow and associated, but slightly delayed thermopeaking effects, and depending on local regulation regimes (see Young, Cech & Thompson 2011 for reviews; Rolls, Leigh & Sheldon 2012; Ellis & Jones 2013; Warren, Dunbar & Smith 2015). 'Beneficial' ecological effects, may include resource subsidies from upstream

reservoir (Ellis & Jones 2013), initially more macroinvertebrate drift (Bruno *et al.* 2013; Bruno *et al.* 2016; Schulting, Feld & Graf 2016), but this may not be sustained (Miller & Judson 2014), maintenance of habitat for spawning and rearing, and biological cues to trigger spawning, hatching and migration (Young, Cech & Thompson 2011). However, more likely adverse effects are increased mortality due to stranding, downstream displacement of fish, and reduced spawning and rearing success due to untimely/obstructed migration and red dewatering (e.g. Saltveit *et al.* 2001; Scruton *et al.* 2008; Young, Cech & Thompson 2011; Auer *et al.* 2017). Hydropeaking also eliminates diel drift patterns when present and leads to substantial invertebrate drift in line with peak flows and rapid temperature changes (Lagarrigue *et al.* 2002; Cereghino, Legalle & Lavandier 2004; Carolli *et al.* 2012).

4.3.   Transient seasons: autumn fish migrations, spawning and egg development

For upstream autumn spawning and downstream spring smolt migrations in salmon and trout, the larger time window is regulated by photoperiod (Quinn, Hodgson & Peven 1997; McCormick *et al.* 1998; Robards & Quinn 2002; Moore *et al.* 2012; Harvey *et al.* 2014). However, water temperature and/or flow may control more local migrations, in particular timing of the spawning ascent in the autumn, although many other *in situ* factors may also contribute (Tetzlaff *et al.* 2008; Thorstad *et al.* 2008; Milner, Solomon & Smith 2012; Cunjak, Linnansaari & Caissie 2013). Spawning time appears to be population specific and locally adapted to winter temperature regimes, to allow hatching and first feeding at the most opportune time in spring (Jensen, Johnsen & Heggberget 1991; Shields *et al.* 2005). Thus spawning is linked to fall water temperature (~1-6°C for peak spawning) (Taranger & Hansen 1993; Jonsson & Jonsson 2009; Riedl & Peter 2013) with earlier spawning in colder rivers. Consequently, a modified winter temperature regime for example by hydropower regulation is likely to modify also timing of spawning. The spawning time-temperature link arises from the fact that the duration of embryonic development primarily depends on number of day-degrees (DD) from spawning to hatching (Fig. 14) (Jungwirth & Winkler 1984; Kane 1988; Elliott & Hurley 1998c). DD is around 320°C at low water temperatures of 2°C, but increasing to about 400°C DD with increasing water temperatures up to 10°C (Fig. 14). Higher winter temperatures in

regulated rivers will result in earlier hatching (Syrjanen *et al.* 2008). Timing of spawning is linked to thermal performance (Jonsson & Jonsson 2009; Shuter *et al.* 2012) such that the larvae emerge at a time in spring that maximizes growth performance the following summer season, but presumably also reduce mortality risk associated with spring runoff and wash-out of larvae resulting in high mortality (Jensen, Johnsen & Heggberget 1991; Elliott 1994; Jensen & Johnsen 1999). On the individual and population level, if spring emergence is either too early or too late, i.e. alevins experience low temperatures and high flows, survival will be reduced (Jensen & Johnsen 1999; Einum & Fleming 2000; Letcher *et al.* 2004; Skoglund *et al.* 2012). For coldwater salmon and trout fall spawning and slow embryonic development during low winter temperatures, permit early hatching and feeding at relatively low spring temperatures (Skoglund *et al.* 2011).
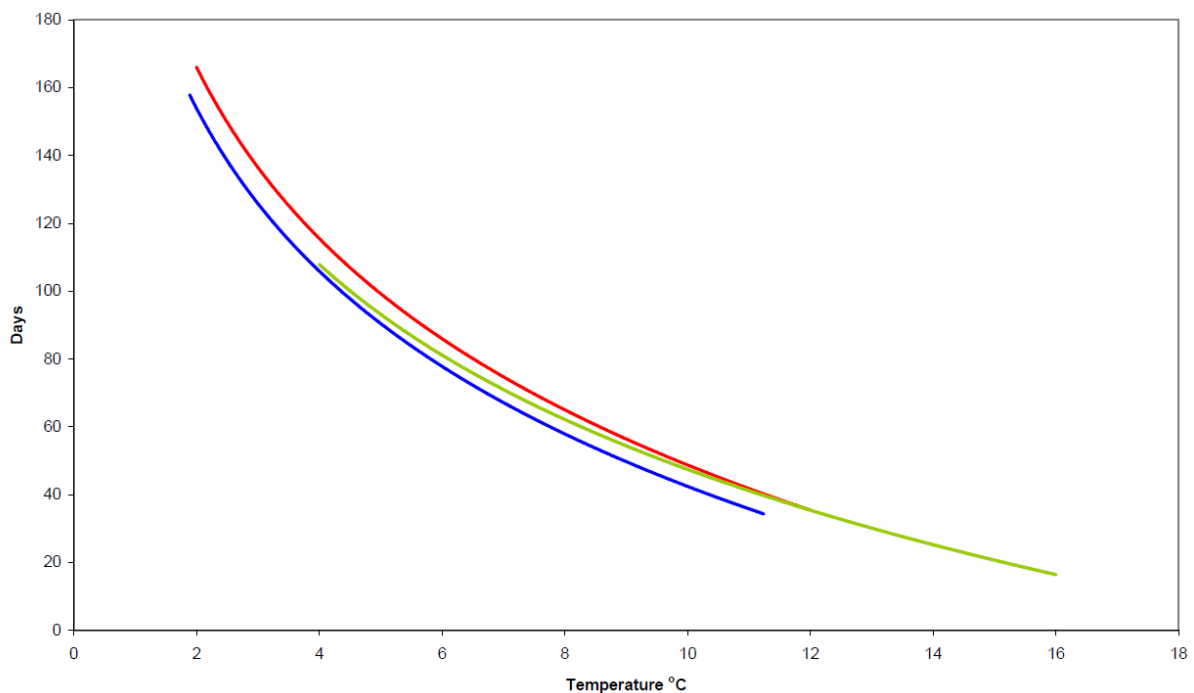
Figure 14. Relationship between incubation temperature and the duration of incubation in brown trout as determined by three independent studies (field and laboratory, several different populations). (From Solomon & Lightfoot 2008).

Because embryonic development is controlled by the number of day-degrees (Fig. 14), timing of emergence may vary greatly among years within a population, mainly because of variations in water temperature contributed by autumn and in particular spring, and with spawning date

as a minor secondary factor (Elliott & Elliott 2010; Cunjak, Linnansaari & Caissie 2013). Like optimal growth temperature, the number of degree-days required from fertilization to emergence may show little adaptive variation among natural Atlantic salmon populations (Heggberget & Wallace 1984; Wallace & Heggberget 1988). Adaptation may rather be reflected in varying spawning times (above), but studies are limited with respect to population gradients studied and results somewhat ambiguous (Jonsson & Jonsson 2009). Effects of incubation temperature on alevin size also appear ambiguous, but with egg size as the major determinant (Elliott & Hurley 1998c). Egg size depends on maternal size, whereas timing of spawning does not seem important (Louhi *et al.* 2015). Egg survival is typically high (Elliott 1994; Barlaup *et al.* 2008; Saltveit & Brabrand 2013; Casas-Mulet, Saltveit & Alfredsen 2015), but variable (Sear & DeVries 2008; Cunjak, Linnansaari & Caissie 2013), depending on a range of biotic and abiotic factors (Greig, Sear & Carling 2007; Gibbins *et al.* 2008; Malcolm *et al.* 2012; Saltveit & Brabrand 2013), including groundwater combined with local hyporheic environments. In the absence of groundwater with sufficient oxygen, egg mortality is likely to be higher with more shallow burial, i.e. more exposure to dewatering and sub-zero temperatures (Casas-Mulet *et al.* 2015; Casas-Mulet, Saltveit & Alfredsen 2015).

4.4.   Spring emergence and early mortality

In contrast to the usually high egg survival, the early stage under and after alevin emergence, is often an important regulatory period with high mortality in salmonid populations (Milner *et al.* 2003; Jonsson & Jonsson 2009; Bret *et al.* 2016), at least in more benign, temperate streams and high-density populations where density-dependent mortality is important (Jonsson, Jonsson & Hansen 1998; Elliott 2009). Emerging individuals in high-density populations may compete for space, with dominance determined by size and aggressiveness. The more aggressive brown trout dominate even larger Atlantic salmon (Einum & Fleming 2000; Einum *et al.* 2011; Skoglund *et al.* 2012). Smaller individuals may be forced to move (Einum *et al.* 2012). Displaced individuals incur high mortalities (Elliott 1994; Einum & Fleming 2000). The presumed larvae size-advantage may, however, in nature be offset by other complex and interacting environmental factors (Robertsen, Skoglund & Einum 2013).

Density-independent abiotic factors such as flow and temperature may be more important in regulating low-density (below carrying capacity) populations in more challenging environments (Elliott 1989; Elliott & Hurley 1998b; Lobon-Cervia & Mortensen 2005; Cunjak, Linnansaari & Caissie 2013; Lobon-Cervia 2014; Bret *et al.* 2016). Higher temperatures may benefit survival, but not extreme temperatures (Gibson & Myers 1988), and correspondingly, low temperatures may negatively affect survival (Elliott 1985; Jensen & Johnsen 1999) in particular if 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 (Syrjanen *et al.* 2008; Skoglund *et al.* 2011). The experimental fry started actively 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, e.g. 8°C for salmon (Jensen, Johnsen & Heggberget 1991). Smaller size and larger energy reserves may be beneficial at low spring temperatures incurring sheltering and cryptic feeding, whereas larger size (from higher incubation temperatures) confer a competitive advantage more beneficial at higher temperatures. Thus higher winter temperatures due to hydropower regulation, may change the local adaptive landscape.

5. LESSONS LEARNED AND GOOD PRACTICE: ENVIRONMENTAL DESIGN OF WATER TEMPERATURE IN REGULATED RIVERS

5.1. Integrating hydro-physical and biological knowledge

Environmental design of water temperature regimes in regulated rivers is challenging and complex. Complexity stems from the substantial number of environmental factors that influence and control water temperature processes in nature and stochasticity in physical-ecological interactions. Moreover, it is frequently challenging because of scarce or lack of baseline data for natural (pre-regulation) conditions. Consequently, environmental assessments are difficult and knowledge is generally limited with regard to the implementation

and consequences of mitigation measures, and the lessons learned. This lack of knowledge, e.g. from systematic before-after control-impact (BACI) studies and from implementation of Strategic Adaptive Management (SAM) to facilitate learning and competence development, leads to uncertainties and general lack of **well-documented mitigation strategies linked to environmental design of water temperatures in regulated rivers.**

For management decisions, the next step for hydro-ecological knowledge, is to also include socio-economic considerations (Acreman 2005). Traditionally, market forces play the most important role in terms of operational decisions, i.e. usually determine the flow regime released. Balancing the demands of hydropower production and environmental protection is, however, becoming increasingly important, e.g. in the Nordic countries. An important driver today and in the foreseeable future is the governmental formal process of revision of (environmental) terms for regulated river systems. Here, the fact that water temperature is a key variable in environmental design of regulated rivers, in combination with the limited quantitative knowledge (see previous chapters), put pressure on decisions about selection of adapted cost-benefit mitigation solutions, both for managers and hydropower operators (e.g. environmental flow and impact on production volume and flexibility for operators). An additional driver is the implementation of the European Water Framework Directive (WFD) (2000/60/EC). The WFD has focus on water quality as one central variable for achieving "good ecological status or potential", which EU members (including economic members) are obligated to achieve within 2023. Water temperature is an important variable in this respect. A challenge here is that expected results and arguments for required implementation of mitigation measures rely to a large extent on the use of modelling tools for integrative methods, which also include economic aspects. Unfortunately, these formal models rarely explicitly include temperature considerations. There are, however, a growing number of more **management**-oriented methods available to also explore and tackle water temperature impacts by hydro-regulation.

Although there has been a consistent focus on general water temperature effects in aquatic ecology, our knowledge is surprisingly limited when it comes to (more specific effects of alternative) mitigation strategies in regulated rivers, and how to quantify actual water temperature alterations and associated environmental impacts. The integration of physical simulation models with models of fish responses into a holistic multi-criteria framework,

including alternative management decisions, is in much needed and in progress This progress is fed by the recent increase in extensive data sets for setup, validation and monitoring of temperatures, based on new technologies for measuring many physical and biological variables. New opportunities are provided by remote sensing techniques like LiDAR (Legleiter *et al.* 2015; Mandelburger *et al.* 2015), thermal river mapping (Dugdale, Bergeron & St-Hilaire 2015), and improved high-resolution tracking techniques for fish (e.g. Stickler *et al.* 2008a; Linnansaari & Cunjak 2013; Weber *et al.* 2016), e.g. acoustic tags with temperature sensors (Ilestad, Haugen & Colman 2012).

Here we outline modelling tools and integrative methods that consider water temperature and ecological responses in rivers. We focus on lessons learned from environmental impacts caused by hydropower regulation and water temperature changes, and emphasize available knowledge from implementation and tests of various mitigation strategies.

5.2. Modelling frameworks and tools for water temperature changes

Seasonal water temperature regimes in regulated rivers are mainly controlled by interactions between local climate processes, hydro power plant operation (flow regimes), local hydrology and river hydraulics (Caissie 2006b; Webb *et al.* 2008a). Numerical modelling of water temperature may, however, be challenging considering data availability (climate, river bathymetry, temperature boundary conditions) and the need for numerical models to cover also small scale temperature variations (e. g. Kurylyk *et al.* 2015). Required model spatio-temporal scale is a general challenge. Environmental assessment and mitigation design often require detailed studies and models on thermal impacts (Kurylyk *et al.* 2015; Corey *et al.* 2017; Garner *et al.* 2017). For example, Garner *et al.* (2017) show the effect of riparian vegetation on energy exchange and temperature on a small stream in Scotland. Furthermore, while most approaches to modelling river temperature are one-dimensional, Carrivick *et al.* (2012) document the potential importance of a two-dimensional approach allowing for simulating spatially distributed temperatures across a river. This will allow for simulation of e.g. thermal refugia and small-scale fluxes of temperature (see Ch. 5 above).

A suite of numerical models for water temperature calculations in combination with models of effects on changing physical and thermal habitat on fish, may be used to assess environmental impacts, but there are still relatively few practical examples (Bartholow 2004; Bustos *et al.* 2017). For example Timalsina, Alfredsen and Killingtveit (2015b) show how a temperature model, an ice model and a model of fish stranding can be used to assess effects of hydropower shutdown during winter. Bakken, King and Alfredsen (2016) combined an hourly temperature model with an egg development model to assess effects of changes in a hydropower operational regime on egg development. This paper also illustrates the accuracy of the temperature model against measured temperature in the river. Calculation of (small-scale) energy balance, lack of pre-regulation data to validate models, development and integration of small-scale thermal (fish) habitat models and validation against fish data, are remaining challenges.

Several numerical hydraulic models have the capacity to simulate one-dimensional water temperature, e.g. the well-known HEC-RAS model (Jensen & Lowney 2004) or the SNTEMP model (Bartholow 1991). These models require detailed data on the river system and its heat balance. An less data-intensive alternative is to use a simplified energy balance model (Toffolon & Piccolroaz 2015; Piccolroaz *et al.* 2016). It relates water temperature to air temperature, but preserves the physical basis of the model. This model is fitted to required observational data, but provides a reasonable simulation only for daily or longer time steps. Recent reviews of alternative statistical models (e.g. regression, auto-regressive, neural network) for stream temperature (Benyahya *et al.* 2007) shows that these models can be alternatives for the full physical approach. Toffolon and Piccolroaz (2015) describe a lumped heat budget model derived from the physical relationships that relate water temperature to air temperature, and shows coherent results for several rivers in Switzerland. The same model has been applied with promising results for river Gaula in Norway (Casas-Mulet, Saltveit & Alfredsen 2016). On a cautionary note, these models need corresponding water and air temperature series for calibration. Hrachowitz *et al.* (2010) describe an empirical, large-scale modelling approach were monthly water temperature is related to landscape controls in the catchment, and suggest the method is suited to understand general effects of changes in land use on temperature regimes. A challenge for all river temperature models, and with specific significance for regulated rivers, is the need to provide the temperature at the boundary of the model domain for the simulation,

when actual measurements are not in place. A time series of temperature at the upstream boundary is important for the simulation of river water temperatures downstream of the tributary or hydropower outlet, and similarly temperature from larger tributaries might also be necessary for a correct simulation. In a regulated system, simulated temperature through the turbine from a reservoir model can be used as input (Gebre, Boissy & Alfredsen 2014). However, temperature measurements are less common for water from the hillslopes of a catchment, from tributaries or for the pre-regulated conditions. One solution is to use a hydrological model to simulate runoff water temperature from climate data (Loinaz *et al.* 2013; Comola *et al.* 2015). Results show a reasonable fit with observations and these methods could be used in more complex temperature simulations where observations are limited. With proper boundary conditions, numerical temperature models may deliver good estimates of water temperature in downstream reaches (Toffolon & Piccolroaz 2015; Bakken, King & Alfredsen 2016)

Application of 1D numerical temperature simulation models require rather detailed data: a number of river cross sections are needed to describe the geometry for the hydraulics, climate data including radiation and cloudiness is needed for the energy exchange, and boundary conditions for flow and water temperature must be provided for the upstream boundary and for all tributaries. (Table 5). These rather extensive data requirements have hitherto limited the application of numerical flow models in management decisions. However, recent advances in data measurement technologies, such as LiDAR and satellite (Lindenschmidt & Chun 2014; Legleiter *et al.* 2015; Müller *et al.* 2017), *in situ* remote-operated sensors and data logging techniques, and more efficient field measurement techniques, reduce required in-stream fieldwork and cost, and increase accuracy (Selker *et al.* 2006; Dugdale 2016). In particular, advances in Airborne LiDAR Bathymetry (ALB) and green laser technology enable us to map river bed topography also in water covered areas with high accuracy (+/- cm level) for entire rivers, and with limited effort and cost (Mandelburger *et al.* 2015). This may, although not yet fully explored, also lead to improved water temperature models, with large potential for evaluating impacts of alternative management decisions and mitigation strategies. However, systematic collection of climate and water temperature data across years for calibration and validation will still be necessary to establish robust data models and impact analysis.

Table 5. Some existing numerical models to simulate water temperature regimes in rivers and lakes.

Model	Characteristics	Experiences	References
HEC-RAS	1D temperature model linked to the much used HEC-RAS model.	Widely applied hydraulic model. Applied in Norway, and temperature model works well with good input.	(Jensen & Lowney 2004; Bakken, King & Alfredsen 2016)
SNTemp	1D model developed by the USGS. Detailed energy balance description in the most comprehensive setup.	Used in several habitat assessment studies and in salmon population studies in the US.	(Bartholow 1989; Bartholow 1991)
MIKE11	1D ice model developed on top of the MIKE11 hydraulic model. Water temperature, ice formation and transport simulations, anchor ice formation.	Handles and fluctuating super critical flow. Shows promising capacities in steep rivers. Applied in Norway.	(Theriault, Saucet & Taha 2010; Theriault & Taha 2013; Timalsina, Charmasson & Alfredsen 2013a)
air2stream	Daily or longer time period statistical model simulating river water temperature as a function of air temperature. The only forcing is air temperature.	Requires calibration data to establish link between water and air temperature. Used in Norway.	(Toffolon & Piccolroaz 2015; Casas-Mulet, Saltveit & Alfredsen 2016)
MyLake	1D lake model that simulates water temperature among other parameters. Can be modified to handle hydropower releases	Modified version used in Norwegian reservoirs. Widely used in lake studies.	(Saloranta & Andersen 2007; Gebre, Boissy & Alfredsen 2014)
CE_QUAL-W2	2D hydrodynamic lake model that can simulate lake temperature. Developed by the US Army Corps of Engineers.	Widely used, also in Norway.	(Bartholow *et al.* 2001)

A more general classification of water temperature regimes, in line with what is available for discharge regimes (e.g. Richter *et al.* 1996; Bevelhimer, McManamay & O´Connor 2014), is complicated, with the general lack of water temperature data, and in particular for pre-regulation conditions (Olden & Naiman 2010a). Therefore, temperature classification methods across regulated systems require temperature models, with their data needs and complexities as outlined above. Olden and Naiman (2010a) used the same classification principles as in the IHA method (Conservancy 2009), but for temperature data for the Flaming Gorge Dam in the US, to document clear changes in magnitude, timing and frequency of temperature pre- and post-dam development. An example of a tentatively more general classification of temperature regimes is by Vanzo *et al.* (2015). They developed indexes for sub-daily temperature fluctuations, and used them to classify river temperature regimes through two indicators, the sub-daily rate of change and the frequency of sub-daily fluctuations. Through these indices, rivers can be grouped into low thermal alteration, moderate thermal alteration and high thermal alteration as a tool for a first classification of thermal impacts.

5.3. Modelling frameworks and tools: integrating water temperature models with biological responses in regulated rivers

For an improved evaluation of environmental impacts related to water temperature alterations in regulated rivers, habitat and/or population models for stream-living organisms, notably fish, need to be integrated with numerical temperature models. Conventionally, fish habitat preference models at different spatial and temporal scales have been widely used as a basis for management decisions, such as the physical habitat simulation system (PHABSIM) (Bovee *et al.* 1998). Fish preferences for relevant habitat factors (usually depth, velocity, substrate) is used as a 'filter' on modelling results of available hydro-physical habitat to generate likelihood of fish presence or not. Water temperature is usually not embedded as a separate factor in these models, because temperature is seen as an external controlling factor. The habitat modelling is only representative for a certain pre-given temperature interval. In a sense, habitat modelling is static within pre-given temperature ranges. As more knowledge is gained regarding fish

behavioral responses to different temperatures (above), there may be a need to integrate also water temperature as a factor in such models to obtain more dynamic modelling. Such hydro-ecological models also have other important limitations (Grimm & Railsback 2013), as they are based mainly on the assessment of species' needs, and do not consider the individual variations in behaviors in which are becoming more evident among e.g. fish populations. Furthermore, habitat use may be confused with habitat preference in these models, variable interactions are rarely included, and links to population growth and survival are uncertain (Garshelis 2000; Railsback, Stauffer & Harvey 2003).

Individual Based Models (IBMs) on the other hand, attempt to model processes that determine survival, growth, and reproduction of individual fish, including competition and habitat effects, and temporal variation on the population level (Railsback, Stauffer & Harvey 2003; Railsback *et al.* 2013). Typically, computer simulations with IBM's include: 1) numerous individuals specified at various scales, 2) decision-making heuristics, 3) learning rules or adaptive processes, 4) an interaction topology, and (5) a non-individual environment. The Norwegian IBM model IBsalmon (Hedger *et al.* 2013b), developed for Atlantic salmon, offers a potential tool to quantify how abiotic and biotic factors affect the individuals of a specific population (Fig. 16). Water temperature is to some extent integrated into this modelling framework for the two probably most important fish developmental processes (above). It is used to compute the time from egg deposition to swim-up and parr growth (Fig. 16). The model has been tested on data from one river (River Nausta, Norway) (Hedger *et al.* 2013b), applied in climate studies (Hedger *et al.* 2013c), and in assessment of mitigation measures on salmon production (Bustos *et al.* 2017).
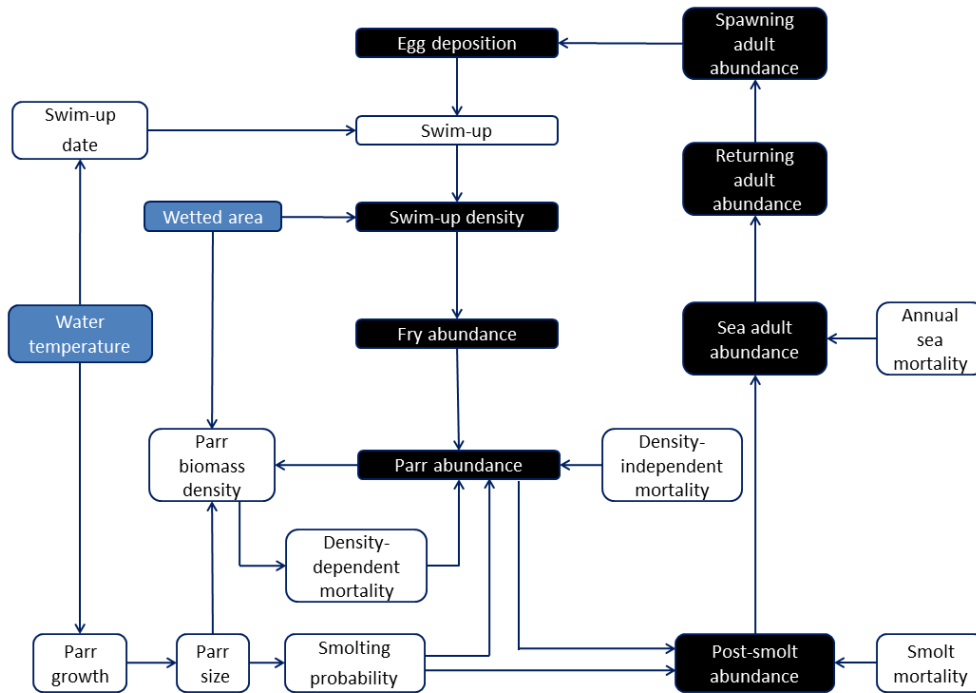
Figure 16. Structure of the IBSalmon model. Modified after (Hedger et al. 2013a). Blue boxes show river variables controlling the salmon population, white boxes show biological processes within the salmon population, and black boxes show salmon population abundances at different life-stages

Many studies combine hydro-physical and biological fish habitat preference models into hydro-ecological models, to explore different water releases and associated ecological scenarios (Mouton *et al.* 2007; Diez-Hernández 2008; Person *et al.* 2014; Guse *et al.* 2015). The implicit assumption is that habitat is an important regulating factor although dependent on local conditions (e. g. Milner *et al.* 2003; Heggenes *et al.* 2016). To what extent abiotic habitat is important relative to biotic population processes, is likely to depend on e.g. how benign the stream environment is (Elliott 1994). Casas-Mulet, Saltveit and Alfredsen (2016) used modelled natural and regulated water temperature in a hydro-peaked river to study the difference in egg development and swim up and how this related to critical habitat availability. Based on results in Casas-Mulet *et al.* (2016), mitigation measures were to avoid dewatering redds in critical cold weather periods and during the alevin stage. Thus, water temperature worked as a tool for defining the timing of hatching and swim-up, and was then combined with hydraulic habitat modelling for assessment of operational potential for different mitigation measures.

5.4.   Mitigating measures

Altered water temperature regimes in regulated rivers may definitely have impacts on aquatic ecology (see Ch. 5). However, lessons learned and effects of good practice of environmental design and targeted mitigation measures are less documented. Existing knowledge is fragmented and even limited with respect mitigation efficiency and mitigation effect. Much of existing knowledge is based on modelling exercises (e. g. Hanna *et al.* 1999; Bartholow *et al.* 2001; Sherman *et al.* 2007), and empirical studies are few (Olden & Naiman 2010a; Poff & Zimmerman 2010; Gillespie *et al.* 2015). Different mitigation measures have been implemented and to some extent tested in regulated systems in (e. g. Bartholow *et al.* 2001; Bennet *et al.* 2011), but often with a theoretical modelling approach, and with limited evaluation and empirical support. Few studies report empirical data for long term biotic responses to environmental variables modified by flow regulation, e.g. temperature (White *et al.* 2017). Such monitoring, evaluation, and reporting are necessary to assess the significance of measured impacts, determine the success of restoration actions, and facilitate ecological learning (Roberts, Anderson & Angermeier 2016). Unfortunately, these steps are too often compromised or omitted from restoration programs (Bash & Ryan 2002). Obviously, this may be caused by inadequate fund, planning or project time line, or a mismatch between temporal scales of flow regulation impacts and monitoring of responses, but all of these may be amended. More serious are lack of pre-project monitoring data and inadequate response variables (Rolls, Leigh & Sheldon 2012; Roberts, Anderson & Angermeier 2016).

There is also the basic question whether one should design mitigation to simulate natural conditions or, if possible and there is a clearly documented potential for it, to improve fish survival/production. Nature usually design the best solutions within the abiotic and biotic frames set. However, if abiotic conditions are shifted, e.g. via hydropower regulation, this may release a potential for improved survival/production. The precautionary principle suggests the former, although much management has focused on the latter, but unfortunately as it turns out, frequently based on insufficient knowledge.

Overall, the main mitigation measures depend on a reservoir supply, and can be divided into i) flexible and/or additional water release strategies from reservoir to mimic natural water temperature conditions (Fig. 17), and ii) methods to increase mixing of surface and bottom water in the water reservoir to smoothen or dampen water temperature differences with depth (Sherman 2000; Kvambekk 2012).
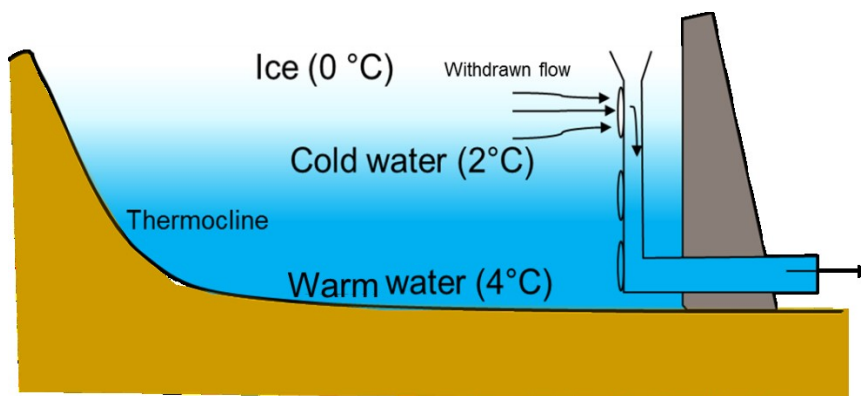
Figure 17. Multi-level intake structure that makes use of the stratification within the reservoir by permitting water with desirable thermal attributes (in this case winter condition, therefore upper layer) to be withdrawn from defined regions within the water column. Modified from (Sherman 2000).

5.4.1. Flexible and/or additional water release from reservoir

Flexible and/or additional water intakes in hydropower dams are a conventional method to mimic natural water temperature variations in regulated rivers. This mitigation measure also known as selective withdrawal, using a multi-level reservoir intake structure, is the most common and most effective way of controlling the water temperature of reservoir releases (Figure 17) (Sherman 2000). In an evaluation report on mitigation measures for temperature mitigation in reservoirs, Sherman (2000) stated that even if the implementation of this measure can have high costs, it is effective, and may be the best opportunity for ecological restoration. Such intake structures provide the opportunity to mimic seasonal variations similar to unregulated conditions (Fig. 17), although some water temperature differences should be expected. This will depend on the water depth for secondary intakes, or regulation

height for flexible intake levels (Fig. 17). Use of flexible and/or additional water releases from a reservoir to mimic natural water temperature regimes, have met with some documented success. In the hydropower regulation system in the Alta River, Norway, a secondary intake was built as part of the construction of the Alta dam in 1987 which was intended to be used for summer temperature control (Asvall & Kvambekk 2001). After regulation, the salmon population in the upper reaches of the river was reduced, possibly because of release of warmer water in winter and reduced surface ice cover (Ugedal *et al.* 2008b) (see Ch. 4). From the winter 2001-2002 (from the start of the winter and as long as it is technically feasible, usually to around the 1st of April), a trial operational regime was initiated. It releases water from the upper intake to lower the downstream water temperature, and reestablish river ice and thereby reduce factors that potentially influenced winter survival of juvenile salmon (Asvall 2008; Ugedal *et al.* 2016). Because of positive results, this was made permanent in 2010. In the river Suldalslågen, Atlantic salmon juveniles experienced reduced spring/summer water temperatures and thereby growth after river regulation. For trial period, an operational regime with reduced production flow was tested to restore river temperatures. This raised temperatures to near the pre-regulation level, but also cost associated with reduced in annual discharge (Kvambekk 2004; Tvede 2006). Olden and Naiman (2010a) shows an example from the Flaming Gorge dam where a multi-level intake was installed in 1978 to mitigate cold water releases from the dam during summer. After installation of the intake, the summer temperature nearly doubled from the period after installing the dam where only a bottom intake was in operation.

Whereas empirical studies on the effects of changed temperature regimes appear to be few, there are a number of modelling studies indicating the feasibility of flexible and/or additional water reservoir intakes for obtaining wanted downstream water temperature regimes. Bartholow *et al.* (2001) used the CE-QUAL-2E model to evaluate the effect of a temperature control device with four intake levels, instead of the original one, installed in the Shasta Lake, California, on the reservoir water quality. Hanna *et al.* (1999) used a similar model setup to evaluate reservoir and downstream temperature, and to show which optimized operation (mixing level) was necessary to meet temperature targets in the downstream river. The cost of this device was 80 million USD (Bartholow *et al.* 2001). Sherman (2000) provide estimated costs of installing various temperature mitigation devices in Australia, together with an

overview of different temperature control devices, and other mitigation measures. Halleraker *et al.* (2007a) used a simple mixing model in Microsoft Excel to compute the effect of a two-level intake in the Follsjø reservoir, Norway, on the outlet temperature, showing the ability to both mitigate increased winter temperature and lowered summer temperature. However, these are modelling exercises. More studies of effects on fish of changes in temperature releases are required. Few exist and most of them have been undertaken in Australia (Miles & West 2011), where differences often may be extreme. For example, Pardo, Campbell and Brittain (1998) found mayfly life history and assemblage structure changes in sites where water temperatures fell by 10-15°C as a result of hypolimnion release during summer.

In an exceptional time series, Vinson (2001) examined 100 years of hydrological and 50 years of aquatic macroinvertebrate assemblage data from the Flaming Gorge dam, Green River, a tributary to Colorado River, USA. A multi-level intake was installed in 1978 to mitigate cold water releases from the dam during summer (see ch. 5 and above). Afterwards, summer temperatures nearly doubled (Fig. 18). 'Reasonable' improvements were also observed for the frequency and duration of thermal events, and the timing of extreme temperatures (Olden & Naiman 2010b), although rate and timing of warming remained different from before dam construction (Vinson 2001). Warmer water led to a 68% increase in insect taxon richness downstream of an intermittent tributary (Red Creek) located 18 km downstream the dam. The actual sampling station (Bridgeport gage) was 26 km downstream. No increase, however, was found in the reach immediately downstream of the dam (0.8 km; Greendale gage).
 Vinson (2001) suggested this apparently lacking response could be explained by the combined effect of three factors: (1) the competitive dominance of insect taxa by amphipods on this reach, (2) low rates of immigration and colonization (from the above reservoir), and (3) 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.
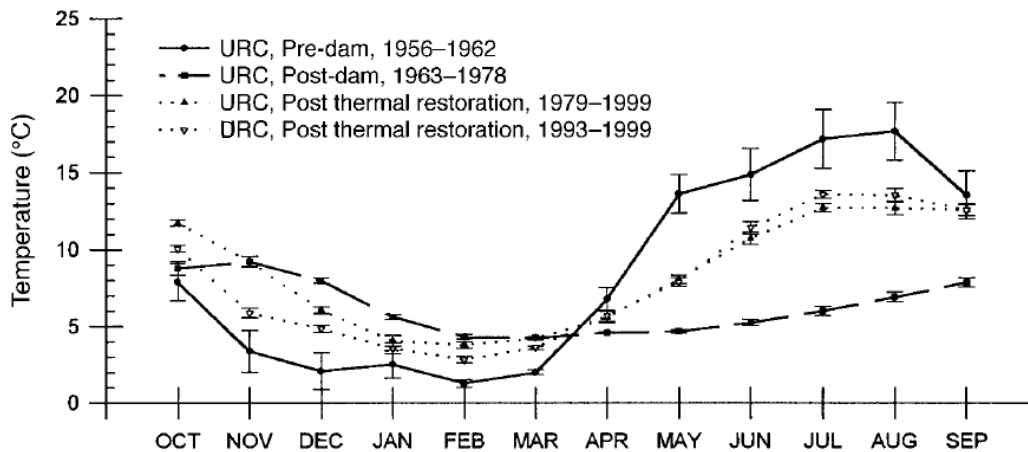
Figure 18. Mean (±1 SE) monthly water temperatures for the Green River for three time periods and two locations, 0.8 km (URC, upstream from Red Creek) and 26 km (DRC, downstream from Red Creek). Modified from (Vinson 2001).

In full scale environmental flow release experiments in a regulated river, Rolls, Leigh and Sheldon (2012) tested effects on fish spawning and recruitment. Unexpectedly, however, varying experimental flow releases did not result in noticeable changes in spawning and recruitment of fish. Temperature effects appeared to override flow effects. Because water was drawn from the cold hypolimnion, summer water temperatures were suppressed. Large experimental releases of impounded water resulted in rapid and sustained declines in water temperature. This likely resulted in a decoupling of simultaneous high flow and temperature that promoted early recruitment in the relevant fish species. Therefore, the study highlights the importance of environmental flow research programs to quantify the impact of regulation on river thermal regimes (Olden & Naiman 2010b; Kvambekk 2012; Rolls, Leigh & Sheldon 2012)

5.4.2.   Methods to increase mixing of surface and bottom water in a reservoir

Sherman (2000) outlines methods for mixing water in a reservoir (destratification) with the purpose of raising temperature in the deeper part of the reservoir where the intake is placed.

One method is to use a bubble plume to create an artificial circulation Fig. 19). The applicability of the method depends on local climate and the size of the reservoir that is to be destratified. Sherman (2000) reports that the cost for the 214 mill. m^3 Lake Samsonvale in Australia is $400.000 for installation and an annual operational cost of $100.000. Another approach is to use surface mounted pumps to pump surface water to the level of the intake or install submerged curtains to force surface water to the intake (Fig. 19). A third method is to hang curtains that prevent cold, deep water from entering the hydropower intakes (Fig. 19).
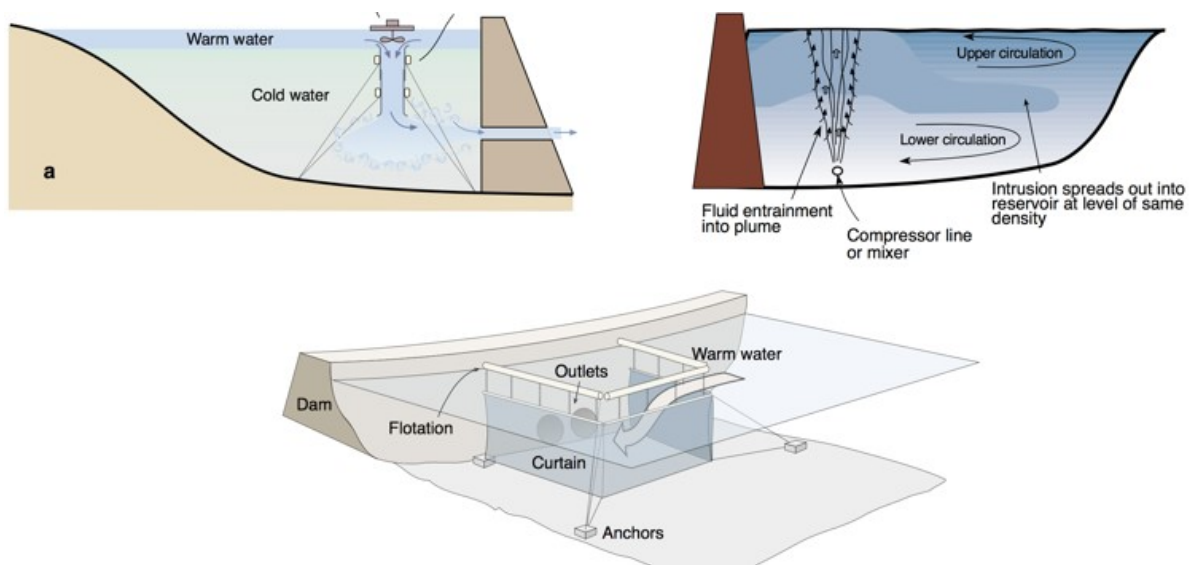
Figure 19. Mixing solutions: a) surface pumping, b) bottom mounted bubbling system, c) submerged curtains.

In a recent thesis, Gray (2016) examined the effects of such thermal curtains that directed warmer surface water to the low-level off-take at Burrendong Dam, Australia. The curtain-directed epilimnial releases raised the water temperatures below the dam with approximately 2°C (mean daily and mean monthly temperature, and diel temperature range). Befroe curtain installment, nutrient concentrations increased at the outlet as a result of hypolimnial releases, with concentrations breaching trigger values indicating ecological disturbance. Direct thermal biological effects were also related to minimum thermal reproductive requirements for local fish species (Fig. 20). Before curtain implementation, the thermal regime from hypolimnial low-level releases was usually not suitable for these native fish. After curtains became operational, thermal ranges were met more frequently.
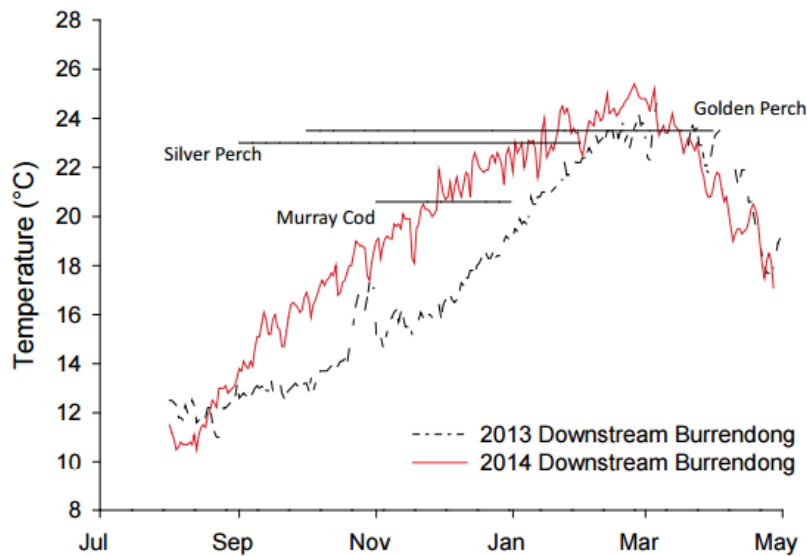
Figure 20. Daily mean temperature (°C) at Downstream Burrendong in the summer months of 2013 (before curtains) and 2014 (after curtains). The three horizontal lines indicate minimum spawning temperature over the spawning period of three native fish in the Macquarie River. From Gray (2016).

Vermeyen (2000) studied the performance of flexible curtains installed in two reservoirs in Sacramento River, California, to reduce the warm water releases that were exceeding critical level for egg incubation and juvenile fish survival. The performance of the curtains (at Lewsiton reservoir) showed a reduction of 1-2°C depending on baseload power releases, with average temperature by decreased about 1.4°C.

6. CONCLUSIONS AND FUTURE RESEARCH

Except for water itself, water temperature is likely the most pervasive factor that affects the abiotic and biotic conditions in aquatic ecosystems. Temperatures have a marked natural seasonal pattern at higher latitude, compared to southern systems with more stable climate. For aquatic organisms, this typically means summer as a season for development and growth,

usually strongly associated with warmer temperatures, with more variable and organism-specific functional effects during the transient fall and spring periods, and the cold northern winter as the season for tolerance, quiescence, starvation, and survival.

Some of the physical properties of water also depends on the seasonal changes in water temperature. The fact that water density is highest at 4°C leads to thermal stratification in lakes. Thus, deep water normally has (depending on water depth, wind and residential time) water temperatures around 4°C year round, but warmer surface waters in summer, and colder in winter. This has important consequences for effects of hydropower regulation. The regulation system is typically either a *high head* system comprising high elevation reservoirs and transfer tunnels, or a *low head* system with run-of-the-river power plants. The latter do not influence thermal regimes much. However, high head systems with storage capacity in upland reservoirs, may lead to major changes from natural water temperatures, because they typically draw reservoir water from the 4°C hypolimnion. In downstream reaches, this results in colder water in summer and warmer water in winter. Pulsed flow regimes generating thermopeaking exceeding natural daily variations in temperatures, are a particular challenge. Such hydropower-related changes in natural temperature regimes, directly affect aquatic biota in an organism-specific variety of ways (see details above).

In Table 6 is a brief overview summary of considerations discussed in this report, with focus on life stages of brown trout and Atlantic salmon. Important considerations are main temperature regulation impacts, potential biological responses and ecological consequences, and potential mitigating measures. Clearly, flexible reservoir intakes and adaptive flow regimes are key mitigating measures with respect to water temperatures.

Table 6. Summary of hydropower regulation water temperature impacts on life stages of brown trout and Atlantic salmon, with likely biologicals responses, ecological consequences, and potential mitigation measures. Question marks indicate knowledge gaps and important research areas. Typically, regulation will increase winter water temperatures. In summer, water temperatures are reduced. It is difficult to generalize about effects of pulsed flows. Effects will depend on local conditions and ramping regime. Increasing number of stars indicate increasing level of confidence.

LIFE STAGE	(POTENTIAL) TEMPERATURE REGULATION IMPACT	(POTENTIAL) BIOLOGICAL RESPONSE	ECOLOGICAL CONSEQUENCES	POTENTIAL MITIGATION MEASURES
EGG INCUBATION PERIOD	Determined by day-degrees (DD). *Warmer winter water shorten incubation period.*	Earlier hatching, later spawning.	Mismatch with environmental conditions.***	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 e. g. 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 alevin.	Mismatch with environmental conditions, e.g. natural spring flows. 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 temperature via flexible water intakes and adaptive flow regime.
FRY TO ADULT FEEDING	Temperature dependent activity. *Slower spring warming, lower summer temperatures.*	Typically reduced feeding. Potentially increased feeding during high summer in warmer climates.	Lower production. Lower juvenile survival.*	Higher spring and early summer temperatures temperature 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 temperature 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 temperature 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.	**	
SMOLT MIGRATION	Several factors (e.g. flow, photoperiod), including temperature. *Slower spring warming.*	Lower trigger temperature (≈ 7-10°C). Delayed smolt migration?	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.*	?	?**	
SPAWNING TIME	Temperature link via DD/egg development. *Warmer winter water shorten incubation period.*	1-8°C. Later spawning.	?*	Timed to optimize early survival in natural streams.

Finally, we summarize suggested future water-temperature and hydropower regulation research and competence needs (see text above for details):

Hydro-physical winter conditions:

- Seasonal and thermal longitudinal effects are neither well studied nor quantified. How extensive are they, and what local conditions (e.g. ground water, 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. Reduced snow and ice cover in regulated streams may expose macroinvertebrates and fish to more open water and frazil ice, but also to increased winter temperatures. How does this affect macroinvertebrates and fish?

- To what extent do different macroinvertebrates survive encasement in ice?

- Is invertebrate production higher in winter-warmer regulated rivers than in the natural state?

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

Biological responses:

- Longitudinal water temperature impacts on fish populations and invertebrate community on the river scale?

- To what extent are there differences both in warm and cold water thermal performance exist 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 regulation, with associated higher water temperatures, resulted in higher parr survival rates and smolt production?

- What are the effects of 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. However, are there any empirical examples?

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

In general, effects of good practice of environmental design and targeted mitigation measures are not well documented. Much of existing knowledge is based on modelling exercises.

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Stay cool
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