

Be cool: A review of hydro-physical changes and fish responses in winter in hydropower-regulated northern streams

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Abstract Winter is an ecologically challenging season for ectothermic cold-water fish in natural streams because of reduced flow and freezing. Hydropower regulation in many northern rivers increase winter stream flow and temperatures, and reduce ice formation and surface ice cover. From a background review of knowledge about e.g. Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) winter survival strategies, we explore responses to hydropower impacts as a basis for adaptive management, mitigating strategies, and future research. Winter intensity and duration, hydrologic conditions and channel characteristics drive complex ice processes which become more complex and pervasive in smaller, high-gradient streams. Stream ice formation may be divided into the dynamic period ‘freeze-up’ in early winter with sub-surface ice, more stable ‘mid-

winter’ with surface ice, and the ecologically challenging ‘ice break-up’ in winter-spring with potential mechanical ice runs and scouring. The characteristics of periods vary depending on climate and hydropower regulation. In reaches downstream of power-plant outlets water temperature may increase and reduce surface ice formation. The mid-winter period destabilize or become absent. In bypass reaches flows decrease and facilitate freezing and ice production. Knowledge about longitudinal water temperature changes is limited. Hydro-peaked systems may aggravate high-low flow effects. A basic winter survival strategy in salmon and trout is energy storage, but also reduced metabolism, tolerance and starvation effected by quiescence. Energy storage may depend on local conditions, but there is little indication of adaptation to local thermal climates. Intraspecific phenotypic plasticity is important. The main behavioural strategy is risk-reducing sheltering in the substratum or deep areas, and nocturnal activity. Local movements between daytime refuges and nighttime slow-current activity areas are usually limited to meters. Larger fish may move more and aggregate in restricted suitable deep-slow refuge habitats such as pools and deep glides. Fish cope with ordinary thermal ice phenomena, and do not appear to become trapped in ice. Surface ice may reduce fish metabolism, but other factors, e.g. availability of substrate shelter, may override this effect. Mechanical ice break-ups and less surface ice may reduce survival. An adaptive mitigating strategy may be higher regulated flows in winter which increase rearing and/or resting habitat and survival, but studies are few and knowledge is limited. However,

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higher regulated flows also affect temperature regime. Low flows increase ice formation, reduce and fragment available habitat, and may reduce egg and fish survival. Influx of ground water may mitigate these impacts, as will stabilize minimum flows. Sudden drops in regulated water discharge should be avoided. Fish may strand, in particular at low temperatures in the daytime when fish are less mobile and seek shelter. The challenging winter season is understudied, and important management considerations and future research areas for better adaptive management are suggested.

Keywords Streams · Winter ecology · Salmon · Trout · Regulation impacts

Introduction

In the seasonal climates of northern Europe and North America, winter is considered a particularly critical season for aquatic organisms (e.g., Power et al. 1999; Huusko et al. 2007; Cunjak et al. 2013), with survival and population size potentially limited by low temperatures, low winter flows and ice phenomena. The predicted winter climate change is milder (1–5 °C increase in average annual temperature), wetter (5–40% increase) and possibly stormier weather (0–8% increase in wind speed) with more frequent, but irregular extreme events. This will particularly affect many snow and glacier-fed streams by increasing runoff, shorter and more unstable winters (up 3 months shorter snow season), and earlier spring flow (e.g., Graham and Harrod 2009; Jonsson and Jonsson 2009; Hanssen-Bauer et al. 2009; Heino et al. 2016). Consequently, more stable cold-water environments may shift to higher altitudes and latitudes, depending on hydro-geography (Hedger et al. 2013b; Filipe et al. 2013; Dugdale et al. 2015). This scenario will likely have severe consequences for cold-water fish, including the widely distributed Atlantic salmon *Salmo salar* (Linnaeus, 1758) and brown trout *S. trutta* (Linnaeus, 1758) (Jonsson and Jonsson 2009; Crozier and Hutchings 2014).

Hydropower regulation also modifies stream flows and temperatures in many northern rivers (e.g., Stanford et al. 1996; Brittain and Saltveit 1989; Olden and Naiman 2010). A renewable resource with substantial societal benefits, hydropower has an installed capacity of 100 GW or more in the Arctic region (Prowse et al. 2011; Anonymous 2016). In Norway with 97%

hydropower of total energy production, two-thirds of all watersheds are affected, contributing about 50% of total reservoir capacity in Europe. In winter, hydropower effects below hydropower plants resemble forecasted climate effects, with increased water flow and temperature, including reduced ice-cover, often with increased frequency of peaking or changing flow. Bypass reaches experience reduced residual or stable environmental flows. The ice effects on river habitat and hydropower systems are extensive both in natural and modified systems (Prowse 2001b; Ettema et al. 2009; Gebre et al. 2013). Ice constitutes a substantial cost to hydropower production (Andersson 1997; Strömshlid et al. 2012; Gebre et al. 2013), and with concomitant thermal and habitat stress on organisms.

The rates of biochemical reactions for ectothermic animals, like cold-water fish such as Atlantic salmon and brown trout, depend on water temperature (Angilletta et al. 2002; Dell et al. 2011), as will associated thermal stress. Basal thermo-tolerance, together with acclimation and behavioral adjustments as two adaptive plastic responses, may mitigate thermal stress in the face of environmental variation (e.g., Elliott and Elliott 2010; Araujo et al. 2013; Gerken et al. 2015). Low temperatures are challenging to thermal physiological tolerances. Furthermore, when water temperatures drops as low as freezing (≤ 0 °C), ice formation occurs, depending on a dynamic and complex interplay among water temperature, water flow, and stream morphology (Prowse 2001b; Turcotte and Morse 2013). Ice generates additional stress through direct hydro-physical changes in the freshwater habitat, e.g., volume and connectivity, and in particular in higher gradient rivers and streams (Stickler et al. 2007; Prowse et al. 2011; Dube et al. 2014), but may also provide benefits, e.g. stable surface ice cover. In colder climates, fitness may reflect the ability of ectothermic organisms like fish to exploit the favorable summer season for recruitment and growth, and physiological and behavioral strategies to survive the unfavourable winter season (Bradshaw et al. 2004; Hedger et al. 2013b).

The natural low temperature winter season may be the limiting ‘season of discontent’ for cold-water fish (Cunjak et al. 1998; Huusko et al. 2007; Cunjak et al. 2013). The hydropower focus has, however, conventionally been on production losses and costs associated with winter ice (Gebre et al. 2013; Gebre et al. 2014), but not biology. Biological implications are important. Organisms may suffer or benefit from natural winter regimes modified

by hydropower, but hydropower regimes may also be modified to meet biological needs. Therefore, based on a background review of natural winter stream conditions and fish responses, the objective of this paper is to focus on (1) how hydropower regulation may impact water temperatures, flows and ice phenomena in winter, and (2) relevant fish biology responses in physiology, behavior and habitat use, with Atlantic salmon and brown trout as model organisms, and (3) relevant mitigating measures.

Natural stream environments in winter

Fish are adapted to their natural stream environments. Responses to hydropower impacts will emerge from their natural resilience to environmental changes. The cold season typically means low water flows, reduced water volumes and velocities, i.e. habitat, but no major change of the physical water properties. Low temperatures *per se* may, however, challenge organisms and infer thermal stress (Angilletta et al. 2002; Elliott and Elliott 2010; Gerken et al. 2015). What really may change the hydro-physical conditions of streams in winter, are the *presence* and *length* of periods of *freezing* temperatures, generating ice, which precipitate hydro-physical changes in water properties and habitat that challenge organisms (Prowse and Ommanney 1990; Prowse 2001b; Huusko et al. 2007; Huusko et al. 2013).

River ice

Ice processes are driven by winter intensity and duration, hydrologic conditions and channel characteristics (Fig. 1). The diverse river ice literature reflects the complexity of

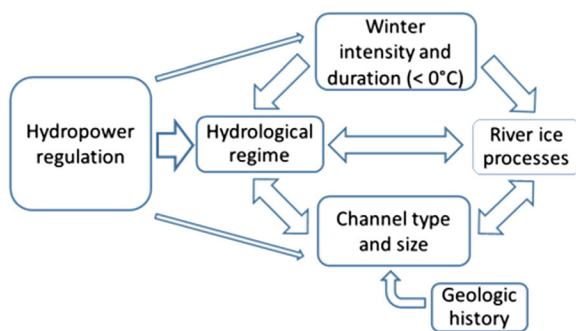


Fig. 1 Main factors influencing ice phenomena and fish habitat conditions in regulated streams in winter (Adapted from Turcotte and Morse 2013)

river ice processes, often with focus on large, low-gradient rivers. They carry more energy and are simpler to understand, predict, and model (e.g., Ashton 1986; Prowse 2001b; Beltaos 2008). However, ice processes vary greatly with channel characteristics, and become more complex and pervasive in smaller, high-gradient streams (Tesaker 1994; Stickler et al. 2008a; Dube et al. 2014) (Fig. 1), i.e. important habitats for salmon and trout, and the majority of stream channel length is usually made up of headwater and lower order streams.

Winter ice formation in streams may be divided into the transient and dynamic period ‘freeze-up’, the more stable ‘mid-winter’, and again transient ‘ice break-up’ in late winter. The duration of periods vary depending on climate, and is often modified considerably by hydropower regulation (Stickler and Alfredsen 2009; Gebre et al. 2013;). In particular the mid-winter period may be long, e.g. more than half of the year in arctic regions, to near non-existing in south temperate climates. Turcotte and Morse (2013) recently summarized a diverse ice literature and suggested a versatile conceptual ice classification model referring it to the more typical natural mid-winter conditions. The model (i) includes winter intensity and duration, (ii) predicts type of ice cover forming in a natural reach depending on characteristics, and (iii) identifies ice processes (see reference for details).

Ice break-up

A good timing index for river ice break-up is the spring 0 °C air temperature isotherm (Prowse et al. 2010). This very dynamic period (Prowse and Culp 2003; Beltaos 2008; Turcotte and Morse 2013) usually constitutes a continuum which may range from a gradual, benign *thermal* transition, e.g. in-place melting of surface ice on stillwater, to *mechanical* break-up events of catastrophic breaking ice-jam fronts, when ice-cover melting is limited and fragmented prior to ice mobilization. Such events with associated bed scour may have physical and ecological effects rarely possible under open-water flow conditions. Mid-winter break-ups are always mechanical (Beltaos and Prowse 2009; Turcotte and Morse 2013). Early spring break-ups tend to be on the mechanical side, whereas late break-ups tend to be thermal, often depending on stream channel gradient.

In *low gradient* stream channels, mechanical break-ups may be caused by sudden rises in discharge and/or incoming ice runs (Turcotte and Morse 2013). The break-up will depend on the dynamic balance between ice cover

(thickness, degradation state) and other resisting forces (e.g. logs, boulders), hydraulic driving forces (discharge, channel gradient), and ice-induced forces (ice rubble pushing, water surface gradient) (Prowse 2001a; Beltaos 2008; Turcotte and Morse 2013).

Less is known about the more complex ice break-up in *steep* channels, which are more prone to suspended ice covers like ice dams (Alfredsen et al. 2006; Stickler and Alfredsen 2009; Dube et al. 2014). Suspended ice cover size, thickness and elevation influence ice break-up (Turcotte and Morse 2013), and may be lifted and mobilized with flow increase. They may then collapse and build up on a downstream ice dam, and finally erupt in an ice front careening downstream in a mechanical break-up. Alternatively, if thick/high, ice dams may resist the incoming suspended ice and melt in place in a more thermal break-up. Thus, break-up in steep channels may be more fragmented, spatially and temporally.

Hydropower regulation impacts in winter

Hydropower regulation modifies the natural winter stream conditions in reaches downstream of power-plant outlets, and in bypass reaches. The stable mid-winter periods may be replaced downstream by repeated unstable transition periods (Stickler and Alfredsen 2009; Gebre et al. 2013) with changed water temperatures, ice features, and water flows (Prowse et al. 2011; Weber et al. 2013). The regulation system and operational strategy are the main drivers behind hydrological 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. 2 top) and 2) the *low head* system or run-of-the-river plant (Fig. 2 bottom). With large storage capacity in reservoirs with thermal stratification, a high head system may lead to major changes in water temperature and flow, through bypassing river reaches, and seasonal flow redistribution and associated temperature changes downstream of the power plant (Olden and Naiman 2010; Dickson et al. 2012). Water temperatures are less affected by low head systems.

Altered water temperature

The winter reservoir temperature gradient is from freezing at the surface to around 4 °C below the thermocline. Drawing water from an intake in the hypolimnion to the

hydropower station will therefore typically raise the water temperature in the downstream river reach during winter, often from around 0 °C to >2 °C (Halleraker et al. 2007; Ugedal et al. 2008) depending on water intake depth and elevation, and reservoir thermal stratification. This increase alters ice dynamics, reduce surface ice, and increase dynamic ice formation downstream. Effects will depend on *in situ* downstream local cooling effects (e.g., ground water, tributaries, in stream river types, gradient), and may persist for several km downstream (Halleraker et al. 2007; Ellis and Jones 2013). 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 (Ugedal et al. 2008). Surprisingly few studies document or quantify downstream longitudinal temperature changes in regulated stream systems in winter, or factors that may influence these changes. Halleraker et al. (2007) combined measured and modelled water temperatures from a reservoir to evaluate downstream temperature effects, resulting from the two alternative mitigation measures, i.e. dual intakes and altered production regime. The mitigation measures reduced water temperatures in winter within the range 0.1–1 °C. For rivers with fluctuating production flows, corresponding fluctuating downstream temperature waves (warm thermopeaking) exceeding natural daily variation in temperature may be expected (King 2010; Zolezzi et al. 2011), but knowledge is limited. Furthermore, because of the delicate balance in water temperature controlling ice production (ice formation regulates on hundredths degree (Stickler et al. 2007), ice dynamics may change on even smaller temporal and spatial scales.

Altered ice conditions and ice break-ups

Hydropower may replace the naturally stable mid-winter period (Gebre et al. 2013) by prolonged transition periods of frazil ice formation and correspondingly unstable or no surface ice cover (Ugedal et al. 2008; Timalsina et al. 2013). The increased frazil production may lead to more anchor ice forming in the river, which can raise water levels and in extreme cases cause local flooding (Lind and Nilsson 2015; Stickler et al. 2010a). Frazil and released anchor ice can accumulate under a downstream ice cover forming hanging dams which change physical habitat in the dam area (Brown et al. 2000), and potentially induce frazil jamming (Allard et al. 2011) and eventually cause midwinter ice break-

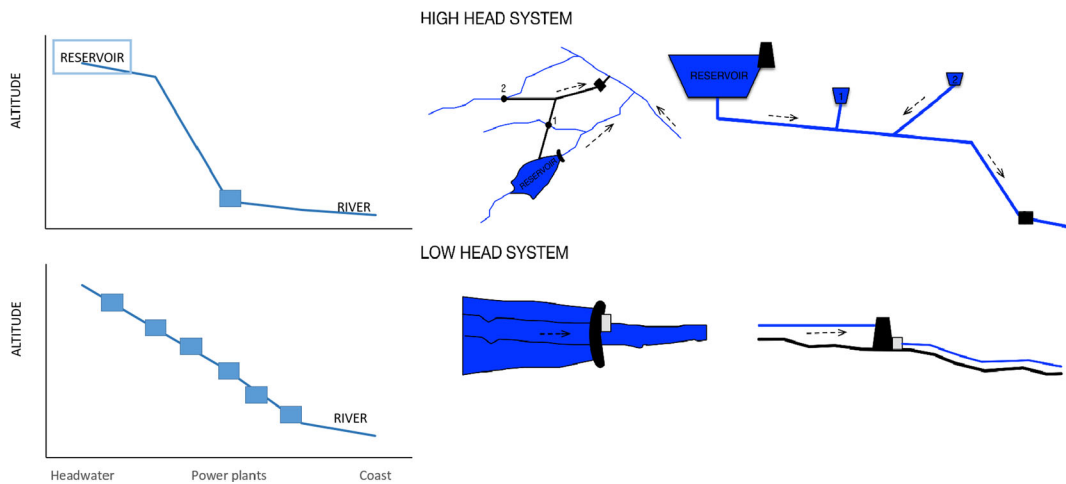


Fig. 2 The two typical hydropower regulation systems. Top: a high head system with a high elevation reservoir, tributary intakes, and transfer tunnels to the power plant. Bottom: a low head or run-of-the-river system with intake and power station in the river dam

ups. On the other hand, it may reduce the possibility of large ice runs on the affected reach due to less and thinner ice formation (Gebre et al. 2013). In systems with bypass reaches, spilled water might trigger ice runs in the bypasses, which may have an ice cover established during low flow conditions (Timalsina et al. 2016).

Altered high and variable flows

Increased flow downstream of hydropower outlets due to releases of production water is typical of high head systems in winter (Fig. 2) (Peters and Prowse 2001; Birkel et al. 2014; Hvidsten et al. 2015a). For example, in Orkla R., Norway, the mean winter waterflow increased from natural about $9 \text{ m}^3 \text{ s}^{-1}$ to about $40 \text{ m}^3 \text{ s}^{-1}$ after regulation in 1983 (Hvidsten et al. 2015b). High flows may initially increase water volume and wetted area (available habitat) (Junk et al. 1989), and also provide nutrient input through flushing (Bowes et al. 2005). However, similar to low flows, *in situ* effects will depend on local stream morphology and flow characteristics.

Hydro-peaked systems tend to aggravate high-low flow effects, depending on down-ramping rate, ramping amplitude, frequency of flow fluctuations, prior flow conditions, and timing of pulse (Young et al. 2011; Ellis and Jones 2013; Warren et al. 2015). Fluctuating flows during freeze-up may influence consolidation events and thereby ice break-ups during cold periods (She et al. 2012). With longer operational stops or by

accidental shutdown, ice may form during the low flow period (Timalsina et al. 2016). This ice may then be broken and flushed downstream when the production is resumed.

Salmon and trout responses to winter

Fish responses to additional hydropower loads with respect to flow, water temperature, and ice, are part of their natural winter strategies (Shuter et al. 2012; Crozier and Hutchings 2014). The common winter survival strategy is energy storage (Fig. 3). Additional potential 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 et al. 1984; Saraniemi et al. 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 get low. Winter strategies are in turn likely to depend on winter season length and severity, with associated changes in hydro-physical habitat affected by ice phenomena and flow changes.

Low temperature physiology: performance and thermal adaptations?

Water temperature controls biochemical reactions and important physiological responses like development and

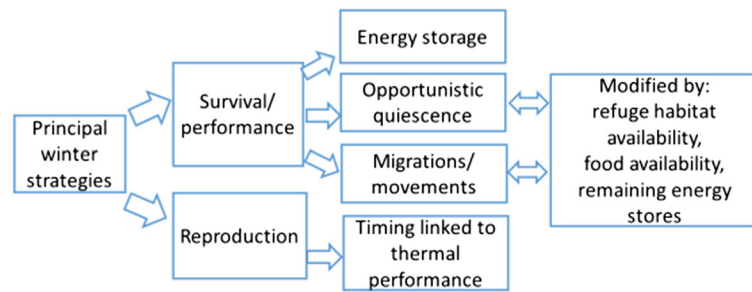


Fig. 3 Principal winter strategies for fish. Energy storage is common in most species. Salmon and trout are not normally able to maintain a positive energy balance by foraging in winter, and therefore adopt a quiescence and starvation strategy. This is opportunistic, and lack of refuge habitat, easily available food and

critically low energy reserves may trigger more activity. Salmon and trout may also migrate to more suitable winter habitats. Both species are fall spawners, and spawning may depend on photoperiod window linked with temperature

growth, and performance of e.g., salmon and trout with temperature is extensively researched (Fry 1971; Elliott 1994; Larsson and Berglund 2006). For example, temperature tolerance for salmon, depending on life stage and individual state, is from 0 to 22–28 °C, but with optimum growth efficiency around 13 °C or so, with the corresponding temperatures for brown trout at 0 to 22–25 °C and c. 9 °C (Tables 1 and 2).

Population differences both in warm and cold water thermal performance exist among salmon and trout (Forseth et al. 2009; Anttila et al. 2013; Hartman and Porto 2014), but it is uncertain to what extent these differences are due to evolutionary adaptation, in addition to phenotypic plasticity. There may be some

genetically based local adaptation to winter climates, notably energy storage (Alvarez et al. 2006; Finstad et al. 2010; Berg et al. 2011; Crespel et al. 2013), but there is little indication of local thermal adaptation or optima in salmon and trout (Jonsson et al. 2001; Forseth et al. 2009; Skoglund et al. 2011; Finstad and Jonsson 2012). Growth capacity may vary among populations, but neither correlates with local natural temperature optima nor indicate counter gradient variation in growth (Jonsson et al. 2001; Larsson and Berglund 2006; Forseth et al. 2009). The apparent lack of local thermal adaptations in Atlantic salmon has tentatively been attributed to the fact that they experience a common thermal environment in the North Atlantic Ocean which may perhaps be more important than freshwater growth in locally different temperature regimes (Forseth et al. 2009). For the more sedentary brown trout, some studies suggest some form of local countergradient adaptation may exist (Finstad et al. 2004b; Nicola and Almodovar 2004; Alvarez et al. 2006), perhaps depending on duration and extremity of temperature environments. Perhaps counter gradient adaptations in (very) cold environments may be important (Finstad et al. 2004b; Nicola and Almodovar 2004; Elliott and Elliott 2010), as some studies have indicated (Jensen et al. 2000; Nicola and Almodovar 2004; Alvarez et al. 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 et al. 1995).

Thus, salmon and trout are physiologically adapted for optimal performance, i.e. best net energy gain, over a specific range of temperatures (Tables 1 and 2) (Clarke

Table 1 Temperature tolerances (°C) for survival of Atlantic salmon and brown trout. (After Elliott and 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

Table 2 Temperature limits (°C) for growth range, optimum growth, and maximum growth efficiency for Atlantic salmon and brown trout. (After Elliott and 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	

Values are for maximum rations. Therefore, optimum will tend to be lower in nature

and Portner 2010; Shuter et al. 2012). Although optimal growth and preferred temperature may be shifted towards the upper end of this window (Portner 2010; Shuter et al. 2012), the definition ‘species-specific preferred temperature’ ± 2 °C seems to work quite well (Magnuson et al. 1979), and may explain population productivity and northern zoogeographic boundaries (Shuter et al. 2012). Most freshwater fish have preferred temperatures well above 4–5 °C (Tables 1 and 2) (Elliott and Elliott 2010; Shuter et al. 2012), whereas winter temperatures are well below that. Energy storage, winter toleration and starvation are therefore the common winter strategies in salmon and trout (Fig. 3). 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).

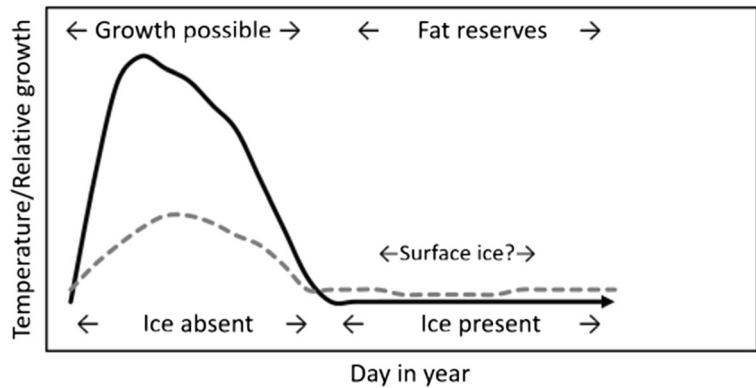
Within salmon and trout populations, variation in thermal tolerance may be substantial depending on developmental stage and individual. The small young-of-the-year are less tolerant to thermal stress (Elliott and Elliott 2010; Breau et al. 2011; Ayllon et al. 2013), and eggs have the lowest tolerance (Elliott and Elliott 2010) (Table 1). Performance limits, expressed as feeding and growth, vary more (Table 2) with differences primarily due to phenotypic plasticity. Atlantic salmon generally appear to have larger growth capacity than trout. Note that the optimum growth temperature will decrease with decreasing energy intake (Elliott and Elliott 2010). At least for relatively benign environmental conditions, growth models e.g. for brown trout, demonstrates the importance of seasonal temperatures (Elliott 2009; Elliott and Elliott 2010). The duration of the cold season

will directly affect fish growth and production in a cold stream (Fig. 4).

Longer winters may to some extent be compensated by 1) build-up of larger fat reserves in summer and 2) lower depletion rates in winter (Figs. 4 and 5) (Shuter et al. 2012). 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). 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 1).

Dynamic active feeding in low temperatures may be controlled by (Fig. 5) (Gotceitas and Godin 1991; Shuter et al. 2012): 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} , $M_{\text{SDAbodymass}}$, F_{access} , U_{rea}), and 4) the obligate energy demand ($M_{\text{basal}} + M_{\text{ParasiteLoad}}$). If the cost of active feeding is larger than the benefit, the best survival strategy is to adopt toleration and starvation. If active feeding is beneficial, then individuals may engage in opportunistic feeding (Metcalf et al. 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). Mortality is

Fig. 4 A season for growth and for tolerance. Solid line represents net energy gain, which will vary locally. Dotted line represents standard metabolism. Winter survival and future reproduction depend on a balance between the relative lengths of the seasons and the fish thermal performance for growth, energy storage and winter quiescence



energy-related and effected through starvation (Finstad et al. 2004c; Naesje et al. 2006).

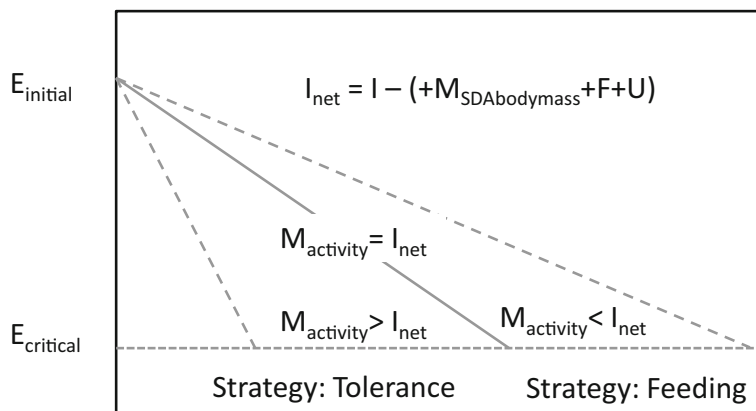
However, low water temperatures and ice formation also affect fish behavior, movement and habitat use, and thereby likely winter survival. Indeed, Huusko et al. (2007) concluded that overwinter survival of juvenile salmonids depends on a complexity of physical and biological factors, appears to be context-dependent, and related to specific habitat characteristics and ice regimes of streams.

Winter behavior and habitat

In winter, salmon and trout behaviors may primarily serve survival, i.e. reduce risk and activity energy expenditure (see e.g., Kemp et al. 2017 for a different result, but for a lenient definition of ‘winter’). Indeed, the basic bio-energetic optimization model may be modified by risk (Reinhardt and Healey 1999) in the form of, in particular predation (Valdimarsson and Metcalfe

1998), and also rapid (frazil) ice formation, one behavior serves both. Thus, salmon and trout tend to become nocturnal and more shelter-seeking in winter (Fraser et al. 1993; Heggenes et al. 1993; Linnansaari et al. 2008; Watz et al. 2014). Typically, as temperatures drop in the fall to 6–8 °C or lower, salmon and trout become less active, seek more shelter in the substratum or deep areas, and become more nocturnal (Rimmer et al. 1984; Cunjak et al. 1986; Heggenes et al. 1993). Consequently, cover and shelter microhabitats become increasingly important at the onset of winter. They reduce swimming activity and maintenance metabolism cost, and predation risk (Valdimarsson et al. 2000; Millidine et al. 2006). Still, the fish respond to direct stimuli, remain active at night, and do not enter any deep torpid state. In streams experiencing freezing and ice phenomena in winter, nocturnalism is important for survival. Notably, during freezing, and before surface ice cover, the heat loss, and frazil and anchor ice formation is greatest at night, when salmon and trout preferably are active. In

Fig. 5 Illustration of a biodynamic optimization model under low water temperatures (winter). (From Shuter et al. 2012)



spite of a number of winter studies salmon or trout trapped in ice have to our knowledge, not been reported.

There may be population differences in temperatures triggering nocturnal behaviors (Valdimarsson et al. 2000). Nocturnalism may also be modified by individual state and feeding motivation (Metcalf et al. 1998; Valdimarsson and Metcalfe 1999) usually driven by hunger. Moreover, salmon become less aggressive at lower light levels (Valdimarsson and Metcalfe 2001) and temperatures, and may become more aggregated in smaller more suitable winter habitat areas (Cunjak et al. 1998; Griffiths et al. 2003). The winter daytime-shelter and nighttime activity behavior remains throughout the winter, and implies limited movements, e.g., for the small recruits ≤ 10 m (Stickler et al. 2008a; Linnansaari and Cunjak 2013). Individual fish usually emerge at night, settle, and then return to their ‘home-stone’.

Systematic active drift feeding in winter appears to be a tenuous proposition for salmon and trout (Fig. 6), because of the reduced feeding efficiency associated with low temperatures and light levels (Fraser and Metcalfe 1997; Valdimarsson and Metcalfe 2001; Piccolo et al. 2014; Watz et al. 2014). This may combine with reduced drift/low feeding resource biomass during the winter season (Brittain and Eikeland 1988; Matthaei et al. 1998; Martin et al. 2001), and possibly also under ice (Bogatov and Astakhov 2011). Still, opportunistic feeding tends to persist (Fig. 6) (Metcalf et al. 1999; Lagarrigue et al. 2002). In more high gradients habitats, e.g. riffles providing important substrate shelter and possibly increased availability of benthic food in winter (Mitro and Zale 2002), benthic winter feeding may be

relatively more profitable than drift feeding, due to the lower cost by not holding station in the current (Fig. 6). Such habitats may represent important winter refuges (Huusko et al. 2007; Stickler et al. 2008b).

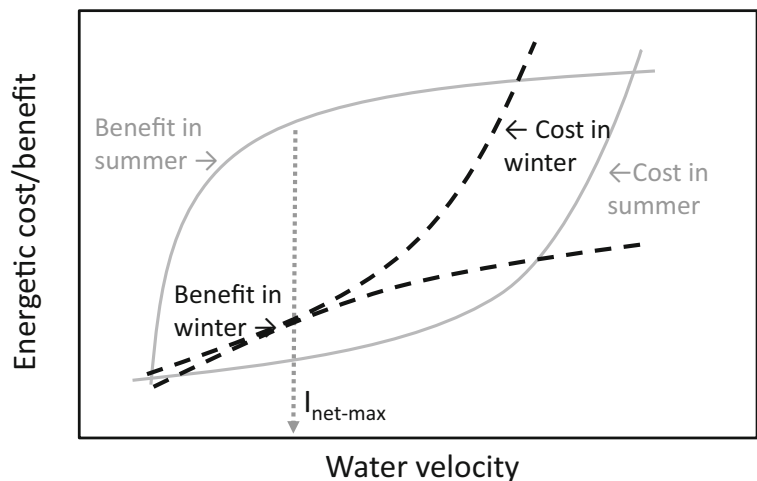
Salmon and trout responses to winter hydropower impacts

Since winter shelter in the substratum is important, increased embeddedness will negatively influence winter habitat quality in regulated rivers. 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 et al. 2008; Linnansaari et al. 2009), thus also increasing energy cost. Availability of shelter may thus override other environmental factors like flow and ice (Stickler et al. 2008a).

Responses to changed ice conditions

Sub-surface ice may develop rapidly at the onset of winter, before the stabilizing surface ice cover establish in regulated streams. Frazil ice may blanket the stream bottom, either as a soft slush or as a hard cover (Stickler and Alfredsen 2009), completely changing the habitat (Heggenes et al. 1993; Brown et al. 2000; Martin et al. 2001), and trigger stress responses. Brown et al. (2000) observed substantial reductions in plasma chloride, sodium and potassium levels and an increase in plasma glucose levels when juvenile rainbow trout experienced

Fig. 6 A conceptual cost-benefit model for drift-feeding salmonids in habitats with low perceived predation risk, in summer (dashed lines) and in winter (solid 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



frazil and anchor ice conditions. Ice formation may trigger avoidance behavior, and fish movements to more suitable habitats (Brown et al. 1994; Brown et al. 2000; Simpkins et al. 2000; Stickler et al. 2007). Rapidly forming sub-surface ice may trap juvenile fish in the substrate and restrict their movement, but juveniles appear to be able to tackle this and avoid being trapped in ice, via behavioural adjustments (Linnansaari and Cunjak 2013). Although it has been suspected (Tack 1938; Brown et al. 1994), there is little indication that frazil ice crystals attach to the gills and affect their respiratory system. In contrast, catastrophic scouring events, e.g., due to hanging ice collapse (Needham and Jones 1959), and sudden mechanistic break-ups, may cause high mortality (Cunjak et al. 2013). That juvenile salmon in general appear to cope well with the more regular thermal ice phenomena (Stickler et al. 2008a; Linnansaari and Cunjak 2013) may seem surprising, considering the harsh winter environments particularly in steep channels (Stickler et al. 2010b; Dube et al. 2014). However, although relevant studies are few because of the difficulties associated with doing direct stream field studies under such extreme conditions, availability of shelter in general may be an important factor during winter for juvenile fish.

Surface ice reduce frazil ice formation (Brown et al. 1994; Linnansaari et al. 2009; Linnansaari and Cunjak 2013), although large accumulations of frazil may still occur in pools and deep areas where flow velocity decreases (hanging dams) (e.g., Prowse 1994). Complete ice and snow cover insulate and stabilize stream ice dynamics. It reduces the amplitude of the short day - long night light regime. However, in northern streams and lakes this do not seem to change diel behavior patterns in local fish fauna (Jurvelius and Marjomaki 2008; Linnansaari et al. 2008; Strand et al. 2008; Linnansaari and Cunjak 2013). Juveniles may even be more active under surface ice, compared to more unstable periods with sub-surface ice or steep channels with more dynamic ice formation (Linnansaari et al. 2008; Stickler et al. 2008a; Linnansaari and Cunjak 2013; Watz et al. 2015).

Northern salmon populations tend to grow better in the dark under the surface ice than their southern cousins (Finstad et al. 2004a), suggesting adaptation. They in turn, grow better in the light without surface ice (Finstad and Forseth 2006). One reason may be reduced resting metabolic rate and stress responses under (simulated) surface ice cover (Finstad et al. 2004a; Watz and Piccolo

2011; Watz et al. 2015). Salmon may also be more active under simulated surface ice, with a higher food intake (Finstad and Forseth 2006; Finstad et al. 2004a; Watz and Piccolo 2011), but results appear ambiguous with respect to increased food intake (Watz et al. 2015). These responses may explain increased mortality of juvenile Atlantic salmon following the loss of ice cover after regulation, and apparently better winter survival in an ice-covered site in River Alta (Johansen et al. 2010; Hedger et al. 2013a). Higher metabolism in ice-free areas may not be offset by higher energy intake, with similarly low prey densities in covered and uncovered habitats (Johansen et al. 2010). Other field studies have not indicated any reduced survival associated with surface ice cover (Huusko et al. 2007; Stickler et al. 2008a). A complex interplay of local habitat factors, e.g. availability of substrate shelter, may override a factorial effect of surface ice alone (Huusko et al. 2007; Stickler et al. 2008b). As spring is approaching, with reduced ice formation and more available habitat, juveniles tend to show reduced site fidelity and move more between habitats (Stickler et al. 2008a; Linnansaari et al. 2009; Linnansaari and Cunjak 2013).

Ice break-up is the final major habitat-hydraulic change in the winter ecology of a stream (Scrimgeour et al. 1994). In regulated rivers, mechanical ice break-ups may occur repeatedly and unpredictably during winter. Such events with their associated physical disturbance effects may certainly cause high mortalities, both in eggs and parr (Cunjak et al. 2013). Unfortunately, few winter mortality studies are, however, able to quantify and separate mortality events.

Water flows

River flow influence key factors like temperature, drift, dissolved oxygen, water quality, sediment scouring, transport and deposition, and habitat availability, type and distribution (e.g., Armstrong and Nislow 2012; Warren et al. 2015). Often low flows up to full wetted width emerge as critical, as wetted width and resulting habitat gain may drop sharply thereafter. Management models currently in use focus on specific low flow cut-off levels, specifically the five percentile flow (Q95), presumably critical to fish production (Gippel and Stewardson 1998; Booker and Acreman 2007). This will, however, be modified by stream physical structure. For a U-shaped riverbed, wetted area will drop sharply below a threshold flow, which may coincide with Q95.

However, for a V-shaped channel form any critical flow may not be identifiable. Such basic patterns are modified by flow-dependent, but likely non-linear changes in water depths and velocities, whereas substrates may change less with increasing flow. These are also important habitat factors for trout and salmon (e.g., Heggenes et al. 1999; Armstrong et al. 2003; Klemetsen et al. 2003). Furthermore, timing or variation in, or frequency and duration of flows in relation to salmon and trout life stage, need to be considered (e.g., Young et al. 2011; Nislow and Armstrong 2012; Warren et al. 2015).

Low winter flows

In contrast to high flow events that may be of limited importance to salmonid production (George et al. 2015) unless they are extreme, low flow events may be critical year round (Elliott et al. 1997; Warren et al. 2015), implying reduced habitat and possibly connectivity, elevated fish densities, increased sedimentation, changed thermal regime and water chemistry. This may present higher risk of hypoxia, temperature stress, and predation, including cannibalism (Heggenes and Borgstrom 1988; Smith and Reay 1991; Vik et al. 2001; Portz et al. 2006), and reduced feeding and growth (Stradmeyer et al. 2008; Brockmark et al. 2010; Reid et al. 2011), resulting in increased mortality (Elliott et al. 1997; Elliott 2006). If habitats are prone to fragmentation, disrupted movements, isolation and increased risk of stranding and desiccation may become a threat (Hunter 1992; Halleraker et al. 2003; Young et al. 2011).

Winter low flows adds to this complexity by increased ice formation, reduced available habitat and associated risk of fish stress and kills (Borgstrom 2001; Huusko et al. 2007; Cunjak et al. 2013). Consequently, low flows in recruitment streams in winter may reduce salmonid production (Elliott et al. 1997; Borgstrom 2001; Elliott 2006; Cunjak et al. 2013; Hvidsten et al. 2015b). Winter low flows and subsequent freezing of dry riverbed areas may significantly increase mortality of fish eggs deposited in the substratum the previous fall. Presence of groundwater influx may increase survival significantly (Casas-Mulet et al. 2015a; Casas-Mulet et al. 2015b). Furthermore, sudden drops in water discharge, associated with hydropower regulation, may result in stranding of salmon and trout leading to increased mortality (Saltveit et al. 2001; Halleraker et al. 2003). Measures taken to minimize such events (e.g., diversion valves, improved operative

routines), combined with changes in intake routines to reduce water temperature and thus increase formation of stable ice cover, may increase juvenile fish survival (Johnsen et al. 2011; Hedger et al. 2013a).

High winter flows

High flows may initially increase available habitat (Junk et al. 1989) and benefit egg and juvenile winter survival in streams (Frenette et al. 1984; Cunjak et al. 2013; Hvidsten et al. 2015b). Restored/increased flows in regulated rivers have resulted in higher salmonid production (Sabaton et al. 2008). Winter high flows may also trigger more activity and movement, in particular high flows during spring ice break-up (Brown et al. 2001), and provide nutrient input through flushing (Bowes et al. 2005). However, *in situ* effects will again depend on fish species and life stage, habitat and flow characteristics. Furthermore, for *in situ* studies in regulated rivers, the effects of higher winter flows are difficult to disentangle from the concomitant increased temperatures and the associated reduction in surface ice and increase in frazil ice formation (above).

Depending on a number of factors (e.g. down-ramping rate and amplitude, frequency and timing of flow fluctuations, prior flow conditions), hydro-peaked systems may aggravate high-low flow effects (see Rolls et al. 2012; Ellis and Jones 2013; Young et al. 2011; Warren et al. 2015 for reviews). Beneficial ecological effects, depending on management regime, may include resource subsidies from upstream reservoir (Ellis and Jones 2013), maintenance of habitat for spawning and rearing, and biological cues to trigger spawning, hatching and migration (Young et al. 2011). More likely adverse effects are increased mortality due to stranding, downstream displacement of fishes, and reduced spawning and rearing success due to untimely/obstructed migration and redd dewatering (above; Young et al. 2011).

Egg incubation and embryonic development in winter

During autumn spawning salmon and trout typically bury their eggs 10–30 cm into river gravels, depending on fish and substrate particle size (Louhi et al. 2008; de Gaudemar et al. 2000; but see Riedl and Peter 2013). Egg burial depth likely also depends on (winter) scour depth and water quality, the latter is often poorer at depth (Youngson et al. 2004). Specific spawning time appears

to be population specific and locally adapted, and linked to water temperature ($\sim 1\text{--}6\text{ }^{\circ}\text{C}$ for peak spawning) (Jonsson and Jonsson 2009; Riedl and Peter 2013) with earlier spawning in colder rivers. Consequently, a warmer winter temperature regime for example due to hydropower regulation is likely to delay timing of spawning, and reduce egg incubation time. The duration of embryonic development depends primarily on number of day-degrees (heat-sum) in winter from spawning to hatching (Elliott and Hurley 1998b). Natural timing of spawning is linked to thermal performance (Jonsson and 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 are not ‘washed-out’ with spring runoff resulting in high mortality (Elliott 1994). If emergence is either too early or too late, survival will be reduced (Einum and Fleming 2000; Letcher et al. 2004; Skoglund et al. 2012). For coldwater salmon and trout fall spawning and slow embryo development during low winter temperatures permit early hatching and feeding at relatively low spring temperatures (Skoglund et al. 2011). However, the heat-sum and thus the timing of emergence may vary greatly among years, mainly because of variations in water temperature, and with spawning date as a minor secondary factor (Elliott and Elliott 2010; Cunjak et al. 2013).

Egg survival over the winter is typically high, typically $>80\%$ (Elliott 1994; Barlaup et al. 2008; Saltveit and Brabrand 2013; Casas-Mulet et al. 2015b), but variable (Sear and DeVries 2008; Cunjak et al. 2013). It depends on a range of biotic and abiotic factors (Greig et al. 2007; Gibbins et al. 2008; Malcolm et al. 2012; Saltveit and Brabrand 2013), e.g., gravel composition, sediment transport, temperature, groundwater influx, and water flow rates. High winter flows leading to mechanical substratum disturbance may generate loss of spawning redds (Barlaup et al. 2008). Egg mortality due to scour and/or mechanical shock may be difficult to observe, but major juvenile fish mortalities associated with mid-winter ice break-up events are documented (Cunjak et al. 2013). Knowledge, however, is limited. In natural systems salmonids may perhaps have evolved to bury their eggs in relatively stable areas that do not typically experience ice or flow scour (Malcolm et al. 2012), or dewatering, to the extent that such events may be predictable. This will be different in regulated systems (Table 4). Low flows during winter may lead to dewatering and freezing of redds and eggs (Table 4), especially if spawning occurs at relatively high flows

(Casas-Mulet et al. 2014; Casas-Mulet et al. 2015b) and the following winter flows are lowered. Mitigating effects of groundwater combined with local hyporheic environments and hydraulic regime confound effects (Malcolm et al. 2012), and *in situ* studies may be required (Becker and Neitzel 1985; Casas-Mulet et al. 2015b). Environmental stress, e.g. mechanical disturbance due to high flows, or low oxygen levels, may induce earlier hatching (Jonsson and Jonsson 2009). Eggs with embryo appear to be the most tolerant egg stage for disturbance (Becker et al. 1982; Neitzel and Becker 1985).

Emergence and early mortality

The early stage under and after alevin emergence in late winter/spring is often an important regulatory period with high mortality in salmonid populations (Milner et al. 2003; Jonsson and Jonsson 2009), at least in more benign, temperate streams and high-density populations where density-dependent mortality is important (Jonsson et al. 1998; Elliott 2009). Emerging individuals may compete for space, with dominance determined by size and aggressiveness, and the more aggressive brown trout dominate the larger Atlantic salmon (Einum and Fleming 2000; Einum et al. 2011; Skoglund et al. 2012). Smaller individuals may be forced to move (Einum et al. 2012), incurring high mortalities (Elliott 1994; Einum and Fleming 2000). Whereas timing of emergence is temperature dependent, alevin and larvae size depend on egg size, which again primarily depend on female spawner size (Elliott and Hurley 1998b; Louhi et al. 2015), but not timing of spawning. The presumed larvae size-advantage may, however, in nature be offset by other complex and interacting environmental factors (Robertson et al. 2013).

Density-independent abiotic factors such as flow, temperature and ice may be more important in regulating low-density (below carrying capacity) populations in more challenging environments (Elliott 1989; Elliott and Hurley 1998a; Lobon-Cervia and Mortensen 2005; Cunjak et al. 2013; Lobon-Cervia 2014). Alevins and young fry are more sensitive than eggs to environmental conditions (Neitzel and Becker 1985), e.g., dewatering and oxygen (Table 4). Studies indicate a positive relationship between water discharge and egg/fish survival (Table 4), e.g., egg and underyearling survival in

Atlantic salmon (Gibson and Myers 1988; Cunjak et al. 2013) and spring flow and brown trout survival (Carline 2006; Lobon-Cervia 2014). Extreme floods during the alevin stage may however, induce ‘wash-out’ and increased mortality (Heggenes 1988; Elliott 1985; Elliott 1994; Jensen and Johnsen 1999). Thus low winter flow and ice, and/or spring high flow at or soon after emergence, may reduce egg and/or juvenile survival (Table 4) (Elliott 1985; Borgstrom and Museth 2005; Cunjak et al. 2013). All of these hydro-physical factors affecting the important early life fish survival are influenced by hydropower regulation, e.g. reduced natural spring peak flows, changed timing and amplitude of spring flows and temperatures, and deserve more study.

Experimental studies on Atlantic salmon indicate that low incubation temperatures produce smaller fry with larger yolk sacs, relative to higher incubation temperatures (Skoglund et al. 2011). The fry started actively feeding with growth even at the lowest temperatures of 2 °C. Smaller size and larger energy reserves may be beneficial at low spring temperatures with sheltering and cryptic feeding, whereas larger size (from higher incubation temperatures) confer a competitive advantage more beneficial at higher temperatures.

Conclusions and future research

Table 3 highlights some likely winter regulation effects. The challenging physical conditions during the cold northern winters are a natural bottleneck for most

organisms living in those environments, including streams. Typical organism responses, e.g. in fish, are tolerance, quiescence, starvation, and survival. Salmon and trout survival in streams depends on a delicate and complex balance between on one hand increasing winter intensity and duration and associated ice phenomena, which reduce survival. This challenge is counterbalanced by the organisms’ energy stores, physiological adaptations, and local, habitat-dependent behavioral adjustments. Hydropower regulation alters the natural environment during winter in complex ways, but usually via increased downstream water temperatures, reduced surface and increased sub-surface ice formation, and increased downstream water flows. However, knowledge about how this affects salmon and trout survival and production is limited. Pulsed flow regimes are a particular challenge, depending on amplitude, ramping rate, frequency, timing, and prior flow, and are difficult to generalize.

In conclusion, winter is the understudied season in running waters (Huusko et al. 2007; Beltaos and Prowse 2009; Gebre et al. 2013), mainly for obvious logistic reasons. Hydropower regulation effects all directly modify stream habitat and thereby fish behavior, survival and production, and generating a variety of biological responses. Hydropower regulation impacts in winter are mainly related to higher downstream water temperatures and flows, or reduced water flow in bypass reaches, and associated changes in ice phenomena (Table 4). Flow and ice directly affect spatial habitat conditions for fish, and thereby fish behavior and activity, but temperature also directly affects fish metabolism (Table 4).

Table 3 Summary of winter regulation effects on water flow, temperature and ice

Variable	Variable state	Negative regulation effect	Positive regulation effect
Flow	High	Higher water velocities, reduced alevin survival	More and stable habitat
	Low	Less habitat, more ice	
	Peaking	Instable habitat, fish stranding, egg desiccation	
Water temperature	High	Higher metabolism, reduced surface ice cover, more subsurface ice	More fish feeding? Earlier start of growing season Higher benthic invertebrate production?
	Peaking	Thermal stress?	
Ice	Surface	Reduced cover, higher fish metabolism	Subsequent increased drift
	Sub-surface	Reduced and unstable habitat	
	Breakup	More frequent, fish and egg mortality during scouring events	

Question marks indicate uncertainty due to limited or lack of knowledge

Table 4 Design and operation of hydropower installations (temperature, flow, intake, outlet) to increase performance of salmon and trout

Stream variable	Regulation impacts	Spatial habitat effect	Biological potential response	Level of certainty for biological response	Potential mitigation alternative	Level of certainty for mitigation effect
Water temperature	Increased downstream (-0.1–3 °C?)	None	Higher metabolism, higher lipid-depletion Increased compensatory feeding activity?	**	Flexible reservoir intake	***
Surface ice	Reduced surface ice cover	Reduced overhead cover	Higher metabolism and perceived predation risk?	**	Flexible reservoir intake	**
Sub-surface ice	Increased frazil ice production and accumulation	Reduced habitat volume and substrate cover	More in-substrate sheltering or movement Reduced survival?	***	Flexible reservoir intake, lower night flows?	***
Ice breakup	Increased frequency and intensity	Scouring, floods	Reduced survival	***	Flow regulation?	*
High flow	Increased level and duration	Increased habitat volume	Increased survival?	**	Stable higher flows	***
Low flow	Reduced level and increased duration in by-pass sections	Reduced habitat quantity, quality, connectivity, increased ice formation	Reduced survival	**	Stable and high minimum flow	***
Pulsed flow	Variable	Bottlenecked by low flows	Reduced survival	**	Reduced amplitude, ramping rate, and frequency	**

Question marks indicate knowledge gaps and important research areas. It is difficult to generalize about effects of pulsed flows, except that it is likely to be negative. Effects will depend on local conditions and pulse flow regime. See text above for detailed explanations and selected references. Increasing number of stars indicate increasing level of confidence

Mitigating measures, primarily flexible reservoir intakes and adaptive flow control, have the potential to approach or restore near-natural habitat conditions (Table 4). In a final short list, this review also identifies some knowledge gaps, i.e. suggested future research areas:

Regulation effects on physical conditions

- Ice phenomena in steep gradient streams, does regulation increase the potential for ice break-ups?
- Development of frazil ice downstream of hydro-power plants; does absence of surface ice change fish habitat conditions?
- Reduced downstream ice cover; how much and does it lead to increased frequency of ice break-ups?
- Downstream longitudinal thermal and ice regimes and changes in regulated stream systems: how extensive and which factors may influence these changes?
- Flow variation; how do flow manipulations affect salmonid emergence and early life survival?

Biological responses to hydro power regulation

- Local/regional thermal adaptations in brown trout and salmon, in particular in northern populations.
- Detailed studies of mortality over the winter; when, where and how fish die.
- Responses to different types of sub-surface ice, surface ice is now better known, but varying surface ice cover in field studies needed; metabolism, fat reserves, body mass, survival.
- Peaking winter temperatures and thermal stress in fish.
- Availability of drift and benthic feed in regulated streams in winter with and without ice cover.
- Profitability of benthic feeding versus drift feeding in winter. Compensatory feeding activity with increased (1–4 °C) winter temperatures and associated lipid-depletion.
- Trout and salmon opportunistic feeding in the temperature range 0–4°C, and with differently adapted populations.
- Habitat preferences in winter and during ice formation – also for modelling purposes.
- Carry-on effects of conditions experienced in early life on later life stages.

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