

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

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Be cool

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fish responses in winter in
hydropower-regulated northern streams**

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University College of Southeast Norway

Kongsberg, 2016

Publication series from the University College of Southeast Norway no. 1

ISSN: 2464-3505 (Online)

ISBN: 978-82-7206-410-4 (Online)



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Abstract

In the seasonal climates of northern Europe and North America, winter is considered a particularly ecologically challenging season for aquatic organisms in natural streams. They experience reduced flow and freezing in winter, with associated hydro-physical changes. In ectothermic animals, like the cold-water fish Atlantic salmon and brown trout, biochemical reactions and behaviors depend on water temperature. Many northern rivers are also impacted by hydropower regulation, which may increase winter stream flow and temperatures, and reduce ice formation and surface ice cover. Knowledge about salmon and trout winter survival strategies and responses to these hydropower impacts is a prerequisite for adaptive management of regulated rivers in winter. The complex ice processes are driven by winter intensity and duration, hydrologic conditions and channel characteristics, and tend to become more complex and pervasive in smaller, high-gradient streams. Winter 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 late winter with potential mechanical ice runs and scouring. The duration of periods vary depending on climate and hydropower regulation, particularly the mid-winter period may change or become absent in regulated streams. An ice classification model may predict type of ice cover forming in a natural reach depending on stream morphology (e.g. gradient, size, and substrate), and winter intensity and duration, and identify ice processes. Hydropower regulation modify natural winter stream conditions, particularly in reaches downstream of power-plant outlets by increased water temperature and reduced surface ice formation, and in bypass reaches by decreased flow and enhanced freezing. The stable mid-winter periods may be replaced by repeated unstable transition periods. High head regulation may increase downstream water flow and water temperature, whereas low head systems may have small or no major impacts on downstream ice conditions. Quantitative knowledge about longitudinal water temperature changes is limited, especially in relation to alternative regulation regimes and intakes/outlets. Hydro-peaked systems may aggravate high-low flow effects, depending on down-ramping rate, ramping amplitude, frequency of flow fluctuations, prior flow conditions, and timing of pulse. A basic winter survival strategy in salmon and trout is energy storage. Their feeding and growth performance is limited at low temperatures, and additional related winter strategies are reduced metabolism, tolerance and starvation effected by quiescence. Energy storage may depend on local conditions, but otherwise there is little indication of adaptation to local thermal climates. Intraspecific phenotypic plasticity is important. The main behavioral

strategy is risk-reducing sheltering and nocturnalism. As temperatures drop to 6-8°C or lower, salmon and trout become less active, seek more shelter in the substratum or deep areas, and are active at night. During freezing and before surface ice cover, the heat loss and associated frazil and anchor ice formation is greatest at night, and visual predators are at a disadvantage. Trout and salmon appear to cope well with 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 breakup may reduce survival. Higher flows in winter may increase rearing and/or resting habitat, which may benefit fish survival, but studies are few. Low flows increase ice formation, reduce and fragment available habitat, and may reduce egg and fish survival. However, influx of ground water may mitigate these impacts during shorter periods with stranding. Sudden drops in regulated water discharge have been demonstrated to 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 night-time slow-current activity areas are usually limited (less than 1m), but with individual variation and single movements up to several kilometers. Larger fish may move more and aggregate in restricted suitable deep-slow refuge habitats such as pools and deep glides. Water temperature and/or flow may control more local spawning/smolt migrations, particularly in smaller streams. In regulated systems, flow during spawning season should not be higher than minimum maintained flow during winter to avoid dewatering and mortality of eggs. Egg development is 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 suitable low flows and available drifting food during and after the 'swim-up' stage. Useful hydro-physical and ice-formation models have been developed to help in impact analysis and adaptive management, but more sophisticated models are often data intensive, and several ice phenomena are still difficult to model. Efforts to integrate biological and societal considerations via e.g. Multi-Criteria Decision Analysis (MCDA), have increased during recent years, but so far met with limited success. In conclusion, potential mitigating measures and research needs are tabulated.

Sammendrag

I det sesongpregede klimaet i Nord-Europa og Nord-Amerika synes vinteren å være en særlig utfordrende sesong for akvatiske organismer i naturlige elver. Vannføringen reduseres og is dannes, noe som også medfører hydrofysiske endringer. For vekselvarme organismer som laks og ørret, er biokjemiske reaksjoner og atferd avhengig av temperatur. Mange elver mot nord er også påvirket av reguleringsinngrep, som kan øke vintervannføringen og temperatur, og derved redusere isdannelse og overflate isdekke. Kunnskap om vinteroverlevelsestrategier hos laks og ørret, og hvordan de responderer på reguleringsinngrep, er et nødvendig grunnlag for miljøtilpasset forvaltning av regulerte elver gjennom vinteren. Is-prosesser i elvene blir styrt av vinterens strenghet og varighet, hydrologiske forhold og elveleiets utforming, og blir ofte mer sammensatte og gjennomgripende i mindre elver med høyere fall. Is-dannelse kan deles inn i først en dynamisk 'fryse' periode med mye is på bunn og i vannsøylen, en mer stabil midt-vinter periode med overflate is, og en ofte økologisk utfordrende avsmeltingsperiode på vår-vinteren med mekanisk og skurende is-gang. Varigheten av disse typiske periodene kan variere avhengig av naturlig klima og reguleringsinngrep, hvor særlig den stabile midt-vinter perioden kan variere mer eller bli helt borte i regulerte elver. En is-klassifikasjons modell kan i noen grad forutsi hva slags prosesser og is-typer som vil dannes i naturlige elver, avhengig av elveleiets utforming (gradient, størrelse, substrat), og av vinterens strenghet og varighet. Reguleringer modifierer de naturlige vinterforholdene, særlig nedstrøms kraftverk ved å øke vannføring og temperatur og redusere dekke med overflate-is. På oppstrøms elvestrekninger med redusert vannføring kan is-dannelse øke. En naturlig stabil midt-vinter periode kan bli erstattet av gjentatte ustabile overgangsperioder. Høyt fall og større vannmengder fører til større vannførings- og temperaturendringer, mens lite fall kan ha små eller ingen vesentlige nedstrøms virkninger. Vi har relativt lite kvantitativ kunnskap om hvor mye og hvor langt nedstrøms like temperaturendringer har betydning, særlig i forhold til alternative reguleringsregimer og plassering av inntak/utløp. Effektkjøring kan forsterke slike effekter, men avhengig av kjørsregime (hastighet og størrelse opp-ned, frekvens, forutgående vannføringsforhold, tidspunkt). Den grunnleggende vinteroverlevelsestrategi for laks og ørret er opplagring av fettreserver. Næringsopptak og vekst er begrenset ved lave temperaturer. Fettreservene spares gjennom nedsatt metabolisme, toleranse og sult, særlig ved at fisken beveger seg lite. Det er lite som tyder på andre lokale tilpassinger til ulike vinterforhold, utover at fisken synes å lagre fettreserver i forhold til forventet vinter. Det er imidlertid stor variasjon mellom individer. For individers atferd er den viktigste strategien om vinteren at laks og ørret søker mer skjul

om dagen og nesten bare er nattaktive. Slik reduseres predasjons risiko og fare for innefrysing. Når temperaturen faller under ca. 6-8°C, blir laks og ørret mindre aktive, søker mer skjul i substratet og i dyp-områder, og blir nattaktive. Ved tidlig frysing, før det dannes overflate-is, er varmetapet og dermed dannelse av sarr og bunnis størst om natten, og predatorer som i hovedsak jakter vha. synet (fugl, ender, mink) også mindre effektive. Laks og ørret ser ut til å tilpasse seg slik isdannelse og blir ikke fanget eller fryser inne i is. Overflate-is kan gi lavere metabolisme, men andre faktorer, f.eks. tilgang på skjul, ser ut til å være viktigere. Mekanisk is-gang kan gi redusert overlevelse. Høyere vintervannføring kan øke tilgang på habitat som kan gi bedre vinteroverlevelse for laks og ørret, men dette er lite undersøkt. Lavere vannføringer øker isdannelse, reduserer og fragmenterer tilgjengelig habitat, noe som kan redusere overlevelse både av egg og fisk. Tilgang på grunnvann kan moderere episodiske tørrleggings effekter. Brå reduksjoner i regulert vannføring kan føre til stranding av fisk, særlig ved lav temperatur om dagen når fisken er i skjul og lite mobil. Lokale forflytninger mellom skjulområder på dagtid og nattlige aktivitetsområder med lavere vannhastigheter er som regel helt lokale (mindre enn en meter for rekrutter), men med stor individuell variasjon (opp til en km). Større fisk kan forflytte seg mer og samler seg i dype, sakteflytende områder. Vanntemperatur kan også kontrollere mer lokale gyte- og smoltvandring, særlig i mindre elver. I regulerte elver bør ikke vannføring gjennom gytesesongen være høyere enn minimum vannføring gjennom vinteren, slik at egg ikke tørrlegges. Eggutvikling er styrt av vanntemperatur. Yngel er følsomme og sårbare, og har ofte høy dødelighet. Overlevelse kan avhenge av en fin balanse mellom passende lave vannføringer og tilgjengelig driv næring ved og etter 'swim-up' når yngelen begynner å ta til seg næring. Nyttige hydro-fysiske og is-dannelses modeller har etterhvert blitt utviklet som tilleggsredskaper for konsekvensutredninger og forvaltningsbeslutninger, men mer detaljerte og avanserte modeller setter store krav til data og en del isfenomener synes ennå vanskelig å modellere. I senere år er det gjort betydelige innsatser for å integrere biologiske og sosiale hensyn, via for eksempel Multi-Criteria Decision Analysis (MCDA), men disse har så langt hatt begrenset suksess. Til slutt gis en oversikt over mulige avbøtende tiltak og behov for videre forskning.

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1. Introduction

Climate determines water temperature and flow in rivers. Climate changes continuously for natural reasons, but recent changes are considered to be anthropogenic (IPCC 2014). In the seasonal climates of northern Europe and North America, winter is considered a particularly critical season for aquatic organisms (e.g. Power, Brown & Imhof 1999; Huusko et al. 2007; Cunjak, Linnansaari & Caissie 2013; Hedger et al. 2013b; Weber et al. 2013). The 21st century predicted winter climate change in northern Europe and North America is milder, wetter and stormier weather, with more frequent extreme events. This will affect in particular many glacier and snow-fed rivers by increased runoff, shorter and more unstable winters, and earlier spring flow (e.g. Graham & Harrod 2009; Jonsson & Jonsson 2009; Heino et al. 2016). Consequently, more stable cold-water environments may 'migrate' to higher altitudes and latitudes, depending on hydro-geography (Filipe et al. 2013; Hedger et al. 2013b; Dugdale, Bergeron & St-Hilaire 2015b). This scenario will likely have severe consequences for cold-water fish, including the widely distributed Atlantic salmon *Salmo salar* and brown trout *S. trutta* (Jonsson & Jonsson 2009; Crozier & Hutchings 2014).

Many seasonal rivers in Northern Europe and North America are impacted by hydropower regulation. Hydropower energy, a renewable resource with substantial associated societal benefits (relatively clean power, flood controls, water supply), has an installed capacity of 100 GW or more in the Arctic region (Prowse et al. 2011; Association 2016). Climate models forecast an increased energy potential in a wetter climate (Hamududu & Killingtveit 2012). Extensive hydropower development in many northern countries implies that flows and temperatures in most running waters are modified by hydropower regulation, e.g. in Norway with 97% hydropower of total energy production, two-thirds of all watersheds are regulated, which contribute about 50% of total reservoir capacity in Europe. A main effect in rivers due to hydro-regulation is a decrease in inter-annual and intra-annual variability of most elements of the flow regime (Renofalt, Jansson & Nilsson 2010; Geris et al. 2015). Winter hydropower effects resemble forecasted climate effects, with increased water flow and temperature, including reduced ice-cover, below hydropower plants, often with increased frequency of peaking. Bypass reaches, however, experience reduced residual or stable environmental flows. Winter, with its high energy demand, is a particularly challenging season because of the complex interactions between hydrology and ecology. The ice effects on river habitat and hydropower systems are complex and extensive both in natural and modified systems (Prowse 2001b; Ettema, Kirkil & Daly

2009; Gebre et al. 2013). Ice constitutes a cost to hydropower production (Gebre et al. 2013), and with concomitant thermal and habitat stress on organisms, but may also provide benefits, e.g. stabilize surface ice cover and increase winter flow. Direct monetary costs for the hydropower producer due to instream ice formation, may be substantial (millions US dollars; Andersson 1997; Strømslid et al. 2012). For example, and Vaskinn (2013) found that frazil formation on trash racks and blocked intakes from ice runs were the dominating issues for reduced production capacity in Norwegian small hydropower plants. A loss of \$1-\$2 million US\$ annually due to frazil formation on intakes was estimated in Sweden (Andersson 1997). Blocking of intakes by ice may cause substantial direct daily losses, e.g. estimated to 100 000 US\$ for a medium-sized Norwegian power plant (Bjoreio) (Lokna 2006), as may ice induced operational restrictions (Strømslid et al. 2012).

In ectothermic animals, like the cold-water fish Atlantic salmon and brown trout, the rates of biochemical reactions depend on water temperature (Angilletta, Niewiarowski & Navas 2002; Dell, Pawar & Savage 2011). Low temperatures are particularly challenging to physiological tolerances. Both basal thermo-tolerance, and acclimation and behavioral adjustments, as two adaptive plastic responses, may mitigate thermal stress in the face of environmental variation (Baird & Krueger 2003; Elliott & Elliott 2010; Araujo et al. 2013; Gerken et al. 2015). When water temperatures drops as low as freezing ($\leq 0^{\circ}\text{C}$), ice formation occurs (Prowse 2001b; Turcotte & Morse 2013). Ice generates additional stress through direct hydro-physical changes in the freshwater habitat, e.g. volume and connectivity, in particular in higher gradient rivers and streams (Stickler et al. 2007; Prowse et al. 2011; Dube, Turcotte & Morse 2014). Such changes depend on a dynamic and complex interplay among water temperature, water flow, and stream morphology (Turcotte & Morse 2013). Consequently, 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 mitigate the effects of the unfavorable winter season (Bradshaw, Zani & Holzapfel 2004; Hedger et al. 2013b).

Therefore, the low temperature winter season is considered the ecologically challenging and limiting 'season of discontent' for cold-water fish like Atlantic salmon and brown trout, which may be impacted on the individual, population and community levels (Cunjak, Prowse & Parrish 1998; Huusko et al. 2007; Cunjak, Linnansaari & Caissie 2013). Anthropogenic climate change and

hydropower regulation can in turn have major impacts on water temperature, flow and ice (Prowse et al. 2011; van Vliet, Ludwig & Kabat 2013; Gebre, Timalsina & Alfredsen 2014). The hydropower focus has conventionally been on production losses and costs associated with winter ice (Gebre et al. 2013; Gebre, Timalsina & Alfredsen 2014), and how to reduce these losses. However, biological implications may be as important, and organisms may suffer or benefit from modified hydropower regimes. Therefore, the objective of this paper is to focus on, with a multidisciplinary approach, (1) how hydropower regulation may impact water temperature, flow 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.

2. Natural stream environments in winter

Fish are adapted to their natural stream environments. Hydropower impacts are too recent to have had any evolutionary effects. Any fish responses to hydropower impacts will therefore, be based in their repertoire of natural responses to environmental conditions. Ice phenomena characterize winter in northern streams.

2.1. Low temperatures and reduced flows

In a seasonal climate, winter is the cold season, but the concept says little about how cold. In a hydro-physical context, the cold season typically means low water flows. Low flows however, may occur at any time year round. Flows may, and depending primarily on channel characteristics, change water volumes and velocities, i.e. habitat, but do not change the physical properties much, although low temperatures per se may challenge organisms and infer thermal stress (Angilletta, Niewiarowski & Navas 2002; Elliott & Elliott 2010; Gerken et al. 2015). What really may change the hydro-physical conditions of streams and rivers in winter, are the presence and length of periods of freezing temperatures, generating ice. We will reserve the concept winter for running waters that experience freezing events in winter that immobilize water as snow and ice, and precipitate hydro-physical changes in water properties and habitat that challenge organisms (Prowse & Ommanney 1990; Prowse 2001b; Huusko et al. 2007; Huusko, Vehanen & Stickler 2013). Moreover, whereas water temperatures remain approximately the same around freezing, the production and type of ice may vary depending on air temperatures and hydraulics in ice-free areas, and thus generate different fish responses.

2.2. River ice

Ice processes are driven by climate, i.e. winter intensity and duration, hydrologic conditions and channel characteristics (Fig. 1). The diverse river ice literature reflects the complexity of river ice processes, often with focus on large, low-gradient rivers. They tend to be simpler to understand, predict, and model (e.g. Ashton 1986; Prowse 2001b; Beltaos 2008). However, ice processes vary greatly with channel characteristics, and tend to become more complex and pervasive in smaller, high-gradient streams (Tesaker 1994; Stickler et al. 2008a; Dube, Turcotte & Morse 2014) (Fig. 1). They are important in the present context.

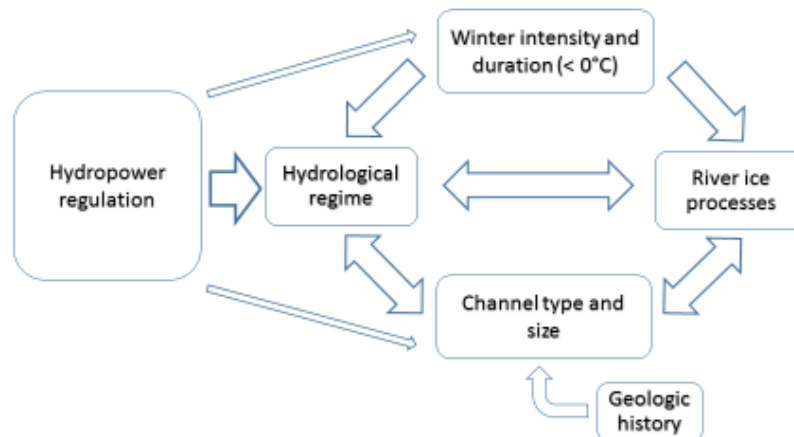


Figure 1. Main factors influencing ice phenomena and fish habitat conditions in streams in winter.

Turcotte and Morse (2013) recently summarized a diverse ice literature and suggested a versatile conceptual ice classification model that (i) predicts type of ice cover forming in a natural reach depending on characteristics, (ii) includes winter intensity and duration, and (iii) identifies ice processes. Winter ice formation and conditions in running waters is often conveniently divided into the transient and dynamic period ‘freeze-up’ in early winter, more stable ‘mid-winter’, and again transient ‘ice break-up’ in late winter. The duration of periods vary depending on climate, and 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. Because Turcotte and Morse (2013) suggest a typology, it is referred to the more typical natural mid-winter conditions. These patterns may be modified considerably by hydropower regulation (below) (Stickler & Alfredsen 2009; Gebre et al. 2013).

The three nominal predictor variables in the model are 1) winter intensity (climate), 2) channel type, and 3) channel size (Table 1, Fig. 2) (Allen 1977; Turcotte & Morse 2013). The four climate categories of increasing winter intensity (Table 1; *Mild*, *Cold*, *Sub-Arctic*, and *Arctic*) may be indicated by cumulative degree-days of frost (CDDF), year-averaged air temperatures (T_{average}) and maximum surface ice thickness (t_{maxthick}) (Allen 1977). The categories may also be associated with the Köppen-Geiger climate classification (see Turcotte & Morse 2013 for details). Although channel types may be categorized using geometry (depth, width), hydraulic (velocity, roughness, Froude number), or

roughness variables (Manning's n , bed grain size), ice processes and types are profoundly different depending on stream gradient. Ice formation in steep streams is more complex, dynamic and diverse (Tesaker 1994; Stickler et al. 2010b; Dube, Turcotte & Morse 2014). Therefore, channel type is categorized by gradient as an operational proxy for stream morphology (Table 1, 2: *Low, Transient, Steep*). (Schumm 1985; Montgomery & Buffington 1997; Bergeron, Buffin-Belanger & Dube 2011). Ice processes may also depend on channel size. Although river ice research has focused on large rivers, which carry more energy, cause larger floods, and are easier to model, the majority of stream channel length is usually made up of headwater and lower order streams (Turcotte & Morse 2013). Channel sizes (Table 1; *Headwater, Intermediate, Wide*) are indicated by bankfull discharge (Q_{bankfull}). Approximate bankfull channel width (W_{bankfull}) may be estimated as $W_{\text{bankfull}} = 4.8 Q_{\text{bankfull}}^{0.5}$ (largely empirical, usually calibrated on a regional basis) (Turcotte & Morse 2013).

Table 1. Overview of conceptual ice predictor variables with associated quantitative indicators (after Turcotte & Morse 2013)

Ice predictor variable	Nominal levels	Indicators				
		<i>CDDF</i>	<i>T_{average}</i>	<i>T^a_{maxthickn}</i>	<i>Ice season</i>	
Winter intensity	Mild	<400	>10°C	<0.25 m	No mid-winter	
	Cold	<1800	>2°C	<1.00 m	Mid-winter breakups	
	Sub-Arctic	<3600	>-6°C	<1.75 m	Long mid-winter	
	Arctic	>3600	>-6°C	>1.75 m		
Channel type	Nominal levels	<i>Channel slope (%)</i>	<i>Flow conditions</i>	<i>Bed material</i>	<i>Channel morphology</i>	
		Low-gradient	<0.1	Subcritical	Sand, small gravel	Dunes and ripples
		Transition Steep	~0.3 >0.5	Mixed Supercritical	Gravel Coarse gravel, boulders	Riffle-pool Cascades, step-pools, rapids
Channel size	Nominal levels	<i>Approximate Q (m³/s)</i>	<i>Approximate W (m)</i>			
		Headwater	<2	<7		
		Intermediate Wide	<200 >200	<70 >70		

^a See (Allen 1977).

Turcotte and Morse (2013) suggest their model framework (Fig. 2A) be used to predict functional ice cover types forming (Fig. 2B) by different ice processes (Fig. 2C) in streams and rivers.

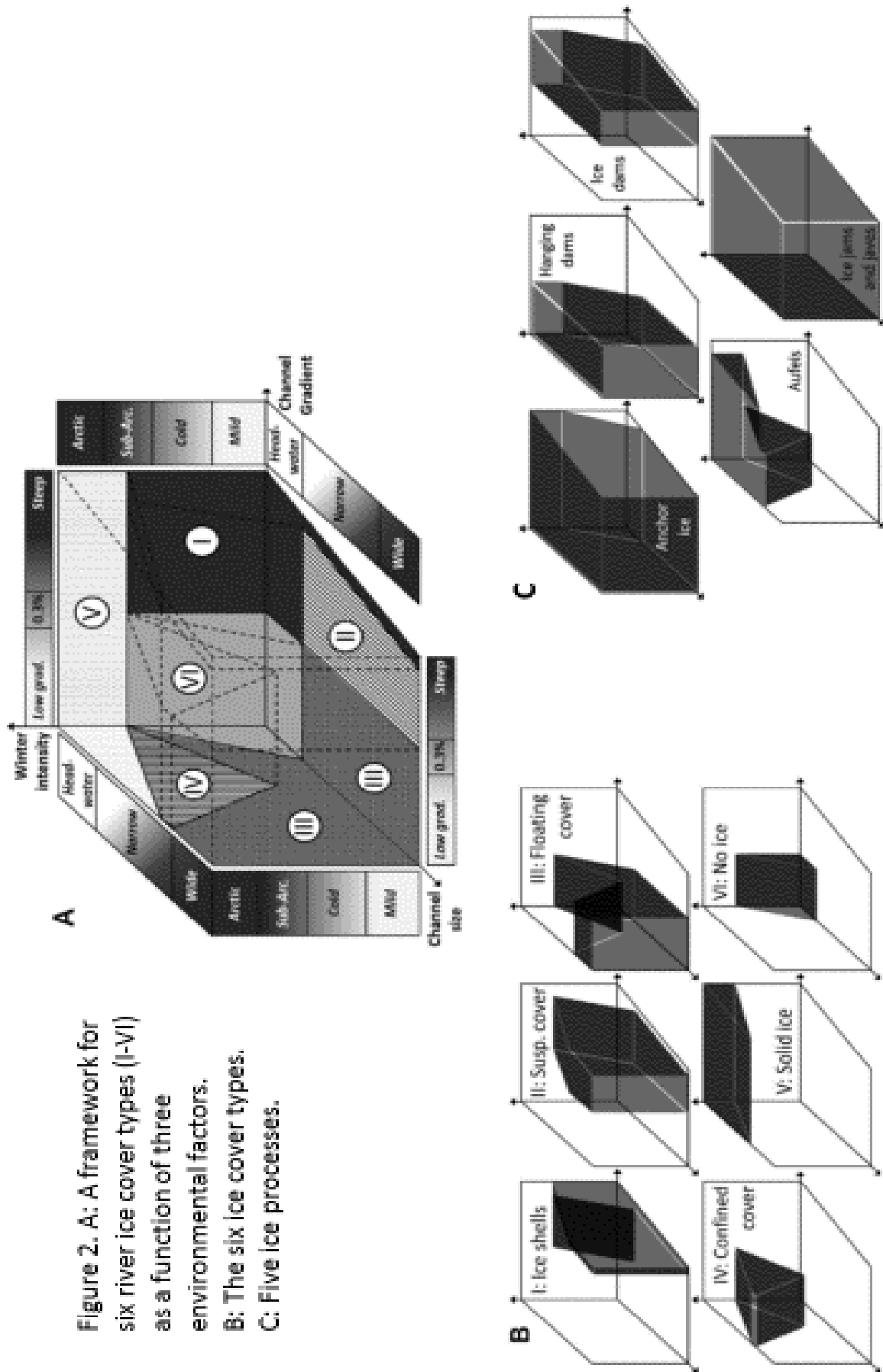


Figure 2. A: A framework for six river ice cover types (I-VI) as a function of three environmental factors.

B: The six ice cover types.

C: Five ice processes.

The model indicates six mid-winter ice-cover types (Fig. 2B): (I) ice shells, (II) suspended ice covers, (III) surface, floating ice covers, (IV) surface, confined ice covers, (V) solid ice, and (VI) no ice. The model indicates five ice processes (Fig. 2C): (AI) active frazil and anchor ice, (HD) passive frazil hanging dams, (ID) ice dams, (AUF) aufeis, and (IJ) ice jams (see Turcotte & Morse 2013 for details). Ice-cover types and processes may all profoundly affect functional stream habitat for organisms, depending on interactions between channel morphology and ice types and ice processes.

2.3. Stream morphology, ice types, and ice processes

To improve the model versatility, and relevant to the context here of stream habitat for organisms in winter, Turcotte and Morse (2013) elaborate on the link between river ice and stream morphology (below, Table 2). This is primarily based on Montgomery and Buffington (1997) longitudinal classification of channel-reach morphology, but also channel patterns as classified by Leopold and Wolman (1957); and Schumm (1985).

Waterfalls generate spray ice shells at freeze-up, less so in mild climates, whereas in cold regions such spray ice shell can cover relatively large waterfalls entirely. Waterfalls may also spray ice crystals in the air and form a “snow cone”, or the ice crystals may drift downstream and generate frazil-saturated flows.

Cascades (gradients 3 to 20%) also tend to form spray ice shells at freeze-up. They may also form anchor ice and ice dams, and develop a partial suspended ice cover in *Cold* regions. In even colder climates, thick ice may accumulate, and possibly develop a complete suspended ice cover and aufeis.

Step-pools (gradients 2 to 8%) are often found downstream of cascades. In *Mild* climates spray ice shells may form, and anchor ice that forms at night is often released after sunrise. As the climate gets colder, large ice dams may develop, and often drown several successive pools. A surface ice cover may form in slow-flowing sections. Extensive icing fields can develop along and over the banks. Ice dams may breach during milder spells, and leave ice covers suspended above the flowing water. The free-flowing water may not be in contact with the ice throughout most of the winter, and the ice coverage may only be partial due to groundwater and head-loss heat contribution. In *Sub-arctic* and *Arctic* climates suspended ice covers may probably cover the entire reach, but few studies on this

exist. Post-freeze-up cold spells can probably cause pressurized flow conditions and aufeis development. Importantly, step-pool reaches of any climate may be affected by ice jams and javes.

Rapids (gradients typically below 4%), particularly in shallow reaches with emerging boulders, can develop anchor ice accumulations, which may be release after sunrise in *Mild* climates. In colder climates, this may accumulate to form ice dams, which in turn may transform the rapid to ice-induced step-pools. In *Cold* climates a partial suspended ice cover may form at freeze-up in *Intermediate* channels. Some section usually remain open, but probably not in more arctic climates. In deeper rapids without emerging boulders, anchor ice may also form, particularly in *Wide* rivers. But the anchor ice will not, according to Turcotte and Morse (2013), emerge at the water surface to create ice dams and a suspended ice cover in Wide rivers. Neither will a floating ice cover develop by frontal progression, but turbulent icing shells that slowly migrate toward the middle of the channel, may develop. Consequently, deep, wide rapids often remain open in winter, continuously producing frazil ice (unless formation of a downstream ice jam lowers the local velocities to permit the formation of a frontal progression ice cover).

Riffle-pool reaches (gradients 0.3 to 2%) represent the transition between Steep channels (riffles, primarily vertical adjustments) and *Low-gradient* channels (pools, lateral adjustments), and exhibit complex ice regimes, involving most ice types and processes. At freeze-up a surface ice cover along the pools first forms, and it may be the only ice forming in *Mild* climates. This floating ice cover does not affect the pool water level much (it is mostly controlled by the downstream riffle), but water velocities may increase as the ice thickens. In colder climates, frazil ice may form in the upstream open water (riffles, rapids), settle at the undersurface of the pool floating ice cover and create hanging dams. In the riffle segments there appears to be four possible freeze-up processes. 1) In *Mild* climates only ephemeral anchor ice and ice shells develop. 2) When colder, anchor ice weirs and dams may form, generating suspended ice cover. 3) In some cases ice-induced braided patterns may slowly develop. Typical are elongated ice “Islands” which are supported by anchor ice accumulation and/or protruding rocks. The open water channels in between gradually freeze by lateral ice development and/or frazil ice clogging, and ice eventually covers the reach. However, this rather slow process may be disturbed, if the water level increases and (some) ice islands, or entire ice covers, are mobilized. 4) If a substantial amount of frazil ice is produced upstream during intense cold nights,

riffles may rapidly (in a few hours) freeze up with a rough ice cover generated by frontal progression. In Sub-arctic and Arctic regions, little is known about mid-winter conditions in riffle-pool channels. Turcotte and Morse (2013) assume, not surprisingly, that such channels develop a complete ice cover, but that ice jam (floating ice cover in pools stall incoming ice runs) and aufeis development is probable.

Meandering riffle-pools (sinuosity above 1.5) typically have short riffles and long, deep pools. At freeze-up the floating ice cover that first develops along pools may partially or completely drown the upstream riffle. Therefore, the ice cover grows faster in meandering channels than in the steeper channel reaches. Thus narrow (*Intermediate*) meandering channels, in the absence of wind/current waves and with little heat storage, tend to freeze up first, before lakes. Anchor ice development is unlikely. Therefore, this habitat presents the least changes in winter to its inhabitants. In *Mild* climates, there may be repeated freeze-melt cycles, whereas in colder climates, a first cold spell may result in a complete ice cover that remains in place, and only thickens, throughout the winter.

In contrast, braided channels, by definition multiple and typically shallow, present an unstable winter habitat, because development of ice shells and anchor ice during freeze-up reduce the flow capacity of each sub-channel. Small changes in ice conditions may generate complete lateral shifts in flow. In mild climates, this process can be repeated several times in winter, resulting in temporarily dry sub-channels and several complete lateral habitat shifts. In colder climates the process may more seasonal, but the freezing and associated flow depletion of some sub-channels and opening up of new, more extensive, and in particular aufeis may develop.

Dune and ripple channels at freeze-up typically develop surface, initially floating ice covers. In colder climates, a confined ice cover can develop in *Intermediate* channels. Aufeis may develop to some extent, but the potential is limited by the low gradient. However, a confined ice cover may be flooded during runoff. Hanging dams and ice jams may occur in Low-gradient reaches if rapids generating frazil ice, are found upstream.

2.4. Ice breakup

As temperature increases in spring, river ice breaks up. A good timing index is the spring 0°C air temperature isotherm (Prowse et al. 2010). Ice breakup is a very dynamic period (Prowse & Culp 2003; Beltaos 2008; Turcotte & Morse 2013). It is usually 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 breakups are always mechanical (Beltaos & Prowse 2009; Turcotte & Morse 2013). Early spring breakups tend to be on the mechanical side, whereas late breakups tend to be thermal, often depending on stream channel gradient.

In *low gradient* stream channels, mechanical breakups may be caused by sudden rises in discharge and/or incoming ice runs (Turcotte & Morse 2013). In general, the breakup process 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 & Morse 2013).

Less is known about the apparently even more complex ice breakup in *steep* channels, which are driven by the same forces as in low gradient channels, but are more prone to suspended ice covers like ice dams (Alfredsen, Stickler & Pennell 2006; Stickler et al. 2008b; Stickler & Alfredsen 2009; Dube, Turcotte & Morse 2014). Suspended ice cover thickness and elevation relative to the water level, and ice dams' size relative to channels width, influence ice breakup (Turcotte & Morse 2013). Such suspended ice formations are easily lifted, and mobilized with flow increase. They may then collapse and build up on a downstream ice dam, and finally erupt in sudden release. This may generate an ice front careening downstream in a mechanical breakup. Alternatively, if e.g. ice dams are thicker/higher than the rising water level, they may resist the incoming suspended ice and melt in place in a more thermal breakup. Thus breakup in steep channels may be more spatially and temporally fragmented.

3. Hydropower regulation impacts in winter

The natural winter stream conditions are often modified considerably by hydropower regulation, particularly in reaches downstream of power-plant outlets, but also in bypass reaches. In many such rivers, the stable mid-winter periods may be replaced by repeated unstable transition periods (Stickler & Alfredsen 2009; Gebre et al. 2013), and with some resemblance to expected climate warming effects.

Hydropower regulation impact natural stream systems in winter by changing 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 (Figure 3 top) and 2) the *low head* system or run-of-the-river plant (Figure 3 bottom). 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. With large storage capacity in reservoirs, a high head system may lead to major changes in both flow and water temperature, through bypassing river reaches, and through seasonal flow redistribution downstream of the power plant outlets (Figure 3a).

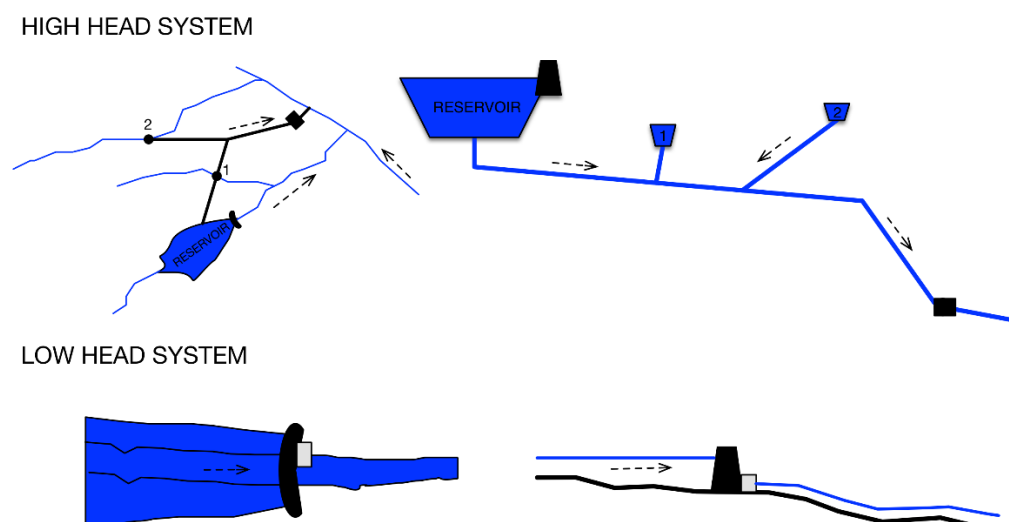


Figure 3. The two typical hydropower regulation systems. Top: a high head system with a high elevation reservoir, tributary intakes, and transfer tunnels to the power plant. Bottom: a low head or run-of-the-river system with intake and power station in the river dam

3.1. Altered water temperature

Changes to the seasonal thermal regime of rivers are common in all types of hydropower regulations with storage capacity. It confers the ability to redistribute flow in receiving waters (Olden & Naiman 2010a; Dickson, Carrivick & Brown 2012). The winter reservoir temperature gradient is from freezing at the surface to around 4°C in the deep layers below the thermocline. Drawing water from an intake in the hypolimnion to the hydropower station will therefore in most cases 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. 2007; Ugedal et al. 2008a). The temperature increase alters downstream ice dynamics, i.e. reduced surface ice and potentially, increased dynamic ice formation. Unfortunately, thermal longitudinal effects are neither well studied nor quantified. It will depend on local cooling effects downstream of the hydropower outlet (e.g. ground water, tributaries, in stream river types, gradient), and may remain for many km downstream (Halleraker et al. 2007; Ellis & Jones 2013). The *in situ* factors controlling cooling and the distance needed to cool water towards the natural water temperature are important to understand, considering the substantial impact zone and physical and ecological effects. Because of the delicate balance in water temperature controlling ice production (ice formation regulates on hundredths degree), changes in ice dynamics may change on small temporal and spatial scales. 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. 2008a). However, and 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 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.

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 this is also understudied.

3.2. Altered ice conditions and ice break ups

Flow and temperature modifications from hydropower operation will modify the natural ice regime in the river system, generating potential technical and environmental issues (Gebre et al. 2013). Of the natural three phases of winter ice conditions in northern streams (freeze-up, stable ice cover, and break-up), particularly the stable mid-winter period can be influenced by hydropower releases (Gebre et al. 2013). This period can be replaced by prolonged transition periods of frazil ice formation and correspondingly unstable or no surface ice cover (Ugedal et al. 2008a). Timalsina, Charmasson and Alfredsen (2013) simulated natural and regulated conditions downstream of a hydropower outlet, and found increased frazil ice formation and an unstable or removed ice cover under the same climatic and morphological conditions. A prolonged ice formation period will lead to cumulatively increased frazil volume. 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 (Stickler et al. 2010a; Lind & Nilsson 2015). Frazil and released anchor ice can accumulate under a downstream ice cover forming hanging dams which changes physical habitat in the dam area (Brown et al. 2000a) and also induce frazil jamming (Allard, Buffin-Bélanger & Bergeron 2011), 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 on the affected reach due to less and thinner ice formation (Gebre et al. 2013). In systems with bypass reaches, however, spilled water might trigger ice runs in the bypasses, which may have an ice cover established during low flow conditions (Timalsina, Becers & Alfredsen 2016).



Photo1: High winter flows downstream of power plants often lead to substantially increased frazil ice formation on colder days.

3.3. Altered high and variable flows

A common effect of high head systems in winter is increased flow downstream of hydropower outlets due to releases of production water from the power plants (Photo 1) (Peters & Prowse 2001; Halleraker et al. 2007; Birkel et al. 2014; Hvidsten et al. 2015a).

High flows may initially increase water volume and wetted area (available habitat), e.g. side channels and floodplain areas (Junk, Bayley & Sparks 1989), and also provide nutrient input through flushing (Bowes, Leach & House 2005). However, similar to low flows, in situ effects will depend on local stream morphology and flow characteristics (below).

Hydro-peaked systems tend to aggravate high-low flow effects, depending on down-ramping rate, ramping amplitude, frequency of flow fluctuations, prior flow conditions, timing of pulse (see Young, Cech & Thompson 2011 for reviews; Rolls, Leigh & Sheldon 2012; Ellis & Jones 2013; Warren, Dunbar & Smith 2015). Warm thermo-peaking, although not yet quantitatively studied, will be a consequence

of fluctuating operation of power plants during the cold period (Zolezzi et al. 2011). Fluctuating flows during freeze-up may influence consolidation events and thereby ice breakups during cold periods (She, Hicks & Andrishak 2012). With longer operational stops or by accidental shutdown, ice may form during the low flow period (Timalsina, Becers & Alfredsen 2016), and this ice may then be broken and flushed downstream when the production is resumed.

4. Salmon and trout responses to winter

Ectothermic native fish are naturally adapted to the challenging low-temperature northern winter climates. Their responses to additional hydropower loads with respect to flows and water temperature and ice, are part of their natural winter strategies (Shuter et al. 2012; Crozier & Hutchings 2014). The common winter survival strategy in most species, including fish, is energy storage (Fig. 4). Since salmon and trout growth performance is limited at lower temperatures (below), 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.

Winter strategies are in turn likely to depend on winter season length and severity, with associated changes in hydro-physical habitat effected by ice phenomena and flow changes. Long term responses will manifest themselves as population variation and eventually population changes. 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, are expected.

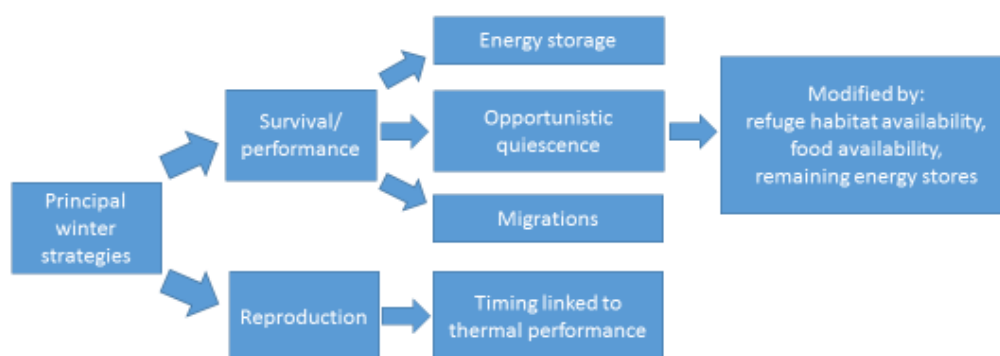


Figure 4. Principal winter strategies for fish. Energy storage is common in most species. Salmon and trout are not normally able to maintain a positive energy balance by foraging in winter, and therefore adopt a quiescence and starvation strategy. This is opportunistic, and lack of refuge habitat, easily 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.

4.1. Low temperature physiology: thermal adaptations, tolerance and performance

In ectothermic animals like fishes, biochemical reactions and important physiological responses like development and growth are controlled by water temperature. Changes in the performance of fish like salmon and trout with temperature is extensively researched (Fry 1971; Elliott 1994; Larsson & Berglund 2006).

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), but it is uncertain to what extent these differences are due to evolutionary adaptation, in addition to phenotypic plasticity. 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). However, in general there is little indication of local thermal adaptation, whereas intraspecific phenotypic plasticity is important in salmon and trout (Skoglund et al. 2011; Finstad & Jonsson 2012).

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). Previous comparative studies on different (juvenile) coldwater brown trout and Atlantic salmon populations have not found much support for a thermal optima adaptation hypothesis (Jonsson et al. 2001; Forseth et al. 2009). Trout and salmon (maximum) growth capacity may vary among populations, but did neither correlate with local natural temperature optima, nor indicate countergradient variation in growth (Jonsson et al. 2001; Larsson & Berglund 2006; Forseth et al. 2009). Instead, adaptive variation in growth potential may be related to factors affecting reproductive success (Forseth et al. 2009; Jonsson & Jonsson 2009; Elliott & Elliott 2010). Some studies have, however, suggested that some form of local countergradient adaptation may exist in brown trout (Finstad, Naesje & Forseth 2004; Nicola & Almodovar 2004; Alvarez, Cano & Nicieza 2006), perhaps depending on evolutionary time, available genetic reaction norms and duration and extremity of temperature environments. To the extent that thermal adaptations have been indicated, countergradient adaptations in (very) cold environments appear important (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). The brown trout have a more sedentary life history and different population-specific thermal regimes throughout its life history may be common. This may suggest a potential for thermal adaptations, 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)

Thus salmonid species are physiologically adapted for optimal performance, i.e. best net energy gain, over a specific range of temperatures (Clarke & Portner 2010; Shuter et al. 2012). An ecologically relevant thermal window (ERTW) has been defined as 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). 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' $\pm 2^{\circ}\text{C}$ seems to work quite well (Magnuson, Crowder & Medvick 1979; termed fundamental thermal niche), and may explain population productivity and northern zoogeographic boundaries (Shuter et al. 2012). Species with lower preferred temperatures are likely to be more efficient foragers during winter conditions. However, most freshwater fish, including the coldwater salmon and trout, have preferred temperatures well above $4\text{-}5^{\circ}\text{C}$ (Table 3, 5) (Elliott & Elliott 2010; Shuter et al. 2012), whereas winter temperatures are well below that. A common effect of high head systems in winter is increased flow downstream of hydropower outlets due to releases of production water from the power plants (Photo 1) (Peters & Prowse 2001; Halleraker et al. 2007; Birkel et al. 2014; Hvidsten et al. 2015a).

Table 3. Temperature tolerances ($^{\circ}\text{C}$) for survival of Atlantic salmon and brown trout. (After Elliott & Elliott 2010).

Life stage	Atlantic salmon		Brown trout	
	<i>Lower</i>	<i>Upper</i>	<i>Lower</i>	<i>Upper</i>
<i>Eggs</i>	0	16	0	13
<i>Alevins</i>				
Long term*	0-2	23-24	0-1	20-22
Short term**	0-1	24-25	0	22-24
<i>Parr and smolt</i>				
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.

Energy storage and winter toleration and starvation are therefore the common winter strategies in salmon and trout. The negligible evidence of intraspecific adaptation for temperature optima may be surprising, but adaptation of enzyme systems to different temperatures appear 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, in particular the alevins (hatched fish with yolk sac) 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) (Table 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 3). Less tolerance of salmon to severe winter climates is reflected in a more limited northern distribution and absence from some glacier-fed rivers, e.g. in Norway. The ultimate lower lethal temperature is for the anadromous form in sea water (Elliott & Elliott 2010). These temperature tolerances remain similar over a wide geographical range with negligible indications of regional adaptations (Elliott & Elliott 2010).

Performance limits, expressed as feeding and growth, vary more (Table 4) with substantial individual and population differences primarily due to phenotypic plasticity. Atlantic salmon generally appear to have larger growth capacity than trout. It is important to note that the optimum growth temperature will decrease with decreasing energy intake (Elliott & Elliott 2010). Values in Table 4 are for maximum rations. Therefore, optimum will tend to be lower in nature.

Table 4. 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
<i>Atlantic salmon</i>				
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
<i>Brown trout</i>				
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, a growth model for brown trout may be a good approximation of growth in natural streams, and it demonstrates the importance of temperature (Elliott 2009; Elliott & Elliott 2010):

$$W_t = [W_0^b + bc(T - T_{LIM})t / \{100(T_M - T_{LIM})\}]^{1/b}$$

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 4), 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 $T_U = 19.48$ (Elliott 2009; Elliott & Elliott 2010). Importantly, if during the growth season, feeding and growth is hampered for some reason, for example by limited habitat during low flows and droughts, trout appear to be able of compensatory growth (Elliott 2009).

The duration of the cold season will directly affect fish growth and production in a cold stream (Fig. 5). 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 (Fig. 4, 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 3).

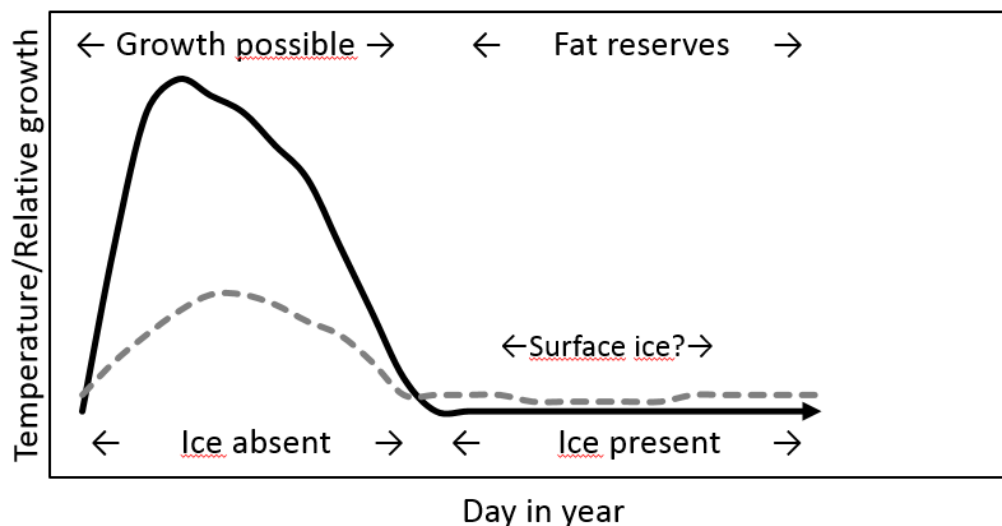


Figure 5. A season for growth and a season for tolerance. Solid line represents net energy gain, which will vary locally. Dotted line represents standard metabolism. Winter survival and future reproduction depend on a balance between the relative lengths of the seasons and the fish thermal performance for growth, energy storage and winter quiescence.

Presumably, active feeding under low temperature conditions ('winter') is controlled by (Gotceitas & 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_{aeces} , U_{rea}), and 4) the obligate energy demand ($M_{\text{basal}} + M_{\text{ParasiteLoad}}$). This translates into a dynamic survival strategy of balancing remaining energy reserves with available prey (Fig. 6). 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, 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).

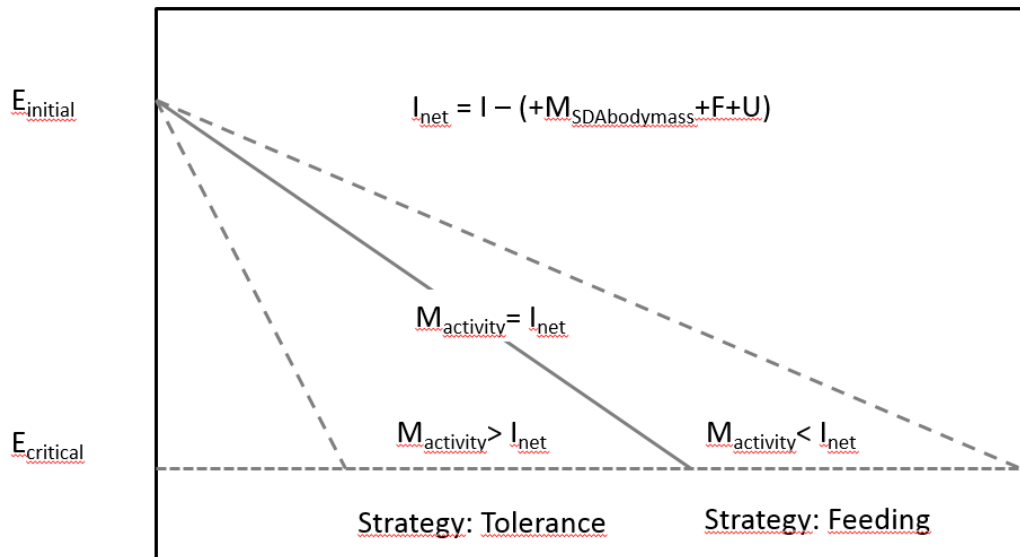


Figure 6. Illustration of a biodynamic optimization model under low water temperatures (winter). (From Shuter *et al.* 2012).

Since active feeding opportunities and growth in salmon and trout are so limited at winter temperatures hovering close to zero in many northern streams, the length of the winter relative to fat reserves and resting metabolic rate, appear critical. Mortality is energy-related and effected through starvation (Finstad *et al.* 2004b; Naesje *et al.* 2006). The severity of the winter will have less direct effect on growth performance. Still, the direct hydro-physical changes related to ice formation will affect fish behavior, movement and habitat use, and thereby likely winter survival. Indeed, in a previous review, 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.

4.2. Winter behavior and habitat

Since foraging during low temperatures in winter is rare for salmon and trout, behaviors in winter are expected to primarily serve survival, i.e. to reduce activity energy expenditure and risk. Indeed, the

basic bioenergetic optimization model appear to be modified by risk (Reinhardt & Healey 1999) in the form of, in particular predation (Valdimarsson & Metcalfe 1998), and also rapid (frazil) ice formation (one behavior serves both). It likely explains the adaptive basis for why salmon and trout tend to become nocturnal and more shelter-seeking in winter (Fraser, Metcalfe & Thorpe 1993; Heggenes et al. 1993; Linnansaari, Cunjak & Newbury 2008; Watz et al. 2014), apparently an important behavioral winter strategy that confers resilience towards the adverse habitat conditions. This *nocturnalism* is triggered by temperatures, and independent of season (Fraser et al. 1995).

Typically, as temperatures drop in the fall to 6-8°C or lower, salmon and trout become less active, seek shelter in the substratum or deep areas more, and become more nocturnal (Rimmer, Paim & Saunders 1984; Cunjak, Power & Barton 1986; Heggenes et al. 1993). Consequently, cover and shelter micro-habitats become increasingly important at the onset of winter. Selection of low-velocity microhabitats reduce swimming activity cost, and also serve to reduce predation risk (Valdimarsson, Metcalfe & Skulason 2000). However, 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, this appears to be a necessary strategy 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 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, presumably local adaptations (Valdimarsson, Metcalfe & Skulason 2000). Nocturnalism may be modified by individual state and feeding motivation (Metcalfe, Fraser & Burns 1998; Valdimarsson & Metcalfe 1999) usually driven by hunger. Salmon also become less aggressive at lower light levels (Valdimarsson & Metcalfe 2001) and temperatures, and may become more aggregated in smaller more suitable winter habitat areas (Cunjak, Prowse & Parrish 1998; Griffiths, Armstrong & Metcalfe 2003). This winter daytime-shelter and nighttime activity behavior remains throughout the winter, and implies limited movements; individual fish usually emerge at night, settle, and then return to their 'home-stone'. If they move to a 'new' home, movements for the small recruits tend to be very limited ($\leq 10\text{m}$) (Stickler et al. 2008a; Linnansaari & Cunjak 2013).

There is also state-dependent individual variation in behaviors, habitat use and related performance (Metcalfe, Fraser & Burns 1998). In Atlantic salmon juveniles in semi-natural environments, individuals with a lower standard metabolic rate used cover more, whereas higher standard metabolic rate were more risk-prone, using areas outside cover more for more successful feeding to compensate higher energy loss (Finstad et al. 2007b).

5. Salmon and trout responses to winter hydropower impacts

Winter shelter in or on the substratum providing low-velocity habitats and cover from predation and ice (Rimmer, Paim & Saunders 1984; Cunjak, Power & Barton 1986; Heggenes et al. 1993), is a basic behavioral in situ response that is important for energy budgets and survival of fish facing changed winter conditions due to hydropower regulation. Therefore, in situ high or increased embeddedness (reduced substrate shelter), e.g. due to increased sedimentation, will negatively influence winter habitat quality in regulated rivers. Lack of shelter increase initial mass loss rates substantially (Finstad et al. 2007a; 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 and ice (Stickler et al. 2008b).

5.1. Responses to ice

Sub-surface ice may develop rapidly at the onset of winter, usually during the early transition period before the stabilizing surface ice cover establish. Frazil ice may blanket the stream bottom and completely change the habitat (Heggenes et al. 1993; Brown et al. 2000b; Martin et al. 2001). Such episodes may 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 frazil and anchor ice conditions. For adult fish, a similar but non-significant pattern in blood plasma was observed. Ice formation may also trigger avoidance behavior, and trout and salmon movements to more suitable habitats (Brown, Stanislawski & Mackay 1994; Brown et al. 2000b; Simpkins, Hubert & Wesche 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 with behavioural adjustments (Linnansaari & Cunjak 2013). Although not well studied, increased mortality in salmon and trout directly due to such freezing phenomena, have to our knowledge not been reported, not even on an anecdotal basis. Catastrophic scouring events, e.g. due to hanging ice collapse (Needham & Jones 1959), and sudden mechanistic breakups may cause high mortality (Cunjak, Linnansaari & Caissie 2013), but in general juvenile salmon appear to cope well with the more regular thermal ice phenomena (Stickler et al. 2008a; Linnansaari & Cunjak 2013). This may seem surprising, considering the harsh winter environments particularly in steep channels

(Stickler et al. 2010b; Dube, Turcotte & Morse 2014) . However, relevant studies are few, which may be explained by the difficulties associated with doing direct stream field studies under such extreme conditions. Also, fish taking refuge in the substrate during such events are not easily observable.

Although it has been suspected (Tack 1938; Brown, Stanislawski & Mackay 1994), there is little indication that frazil ice crystals attach to the gills and affect the respiratory system of salmon and trout. Frazil ice events may benefit fish by increasing 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 allochthonous organic material in the autumn (Hildebrand 1974; Vannote et al. 1980; Dekar, Magoulick & Huxel 2009). Drift may often be light dependent with higher drift at dusk and night than during day (Elliott 1965; Neale et al. 2008; Oberrisser & Waringer 2011). However, this periodicity appears plastic and may break down during continuous summer light at northern latitudes , 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).

Surface ice affects salmon and trout behavior and habitat. Shelter and cover are important habitat factors in winter (above). Habitat may be less prone to frazil ice formation under surface ice cover (Brown, Stanislawski & Mackay 1994; Linnansaari et al. 2009; Linnansaari & Cunjak 2013), although large accumulations of frazil may occur in pools and deep areas where flow velocity decreases, known as hanging dams (e.g. Prowse 1994). Complete ice and snow cover will insulate and stabilize stream ice dynamics, but also reduce the amplitude of the short day - long night light regime. Presence of surface ice and snow cover on northern streams and lakes do not seem to change diel behavior patterns in local fish fauna, which continue to correlate with above-surface photoperiod (Jurvelius & Marjomaki 2008; Linnansaari, Cunjak & Newbury 2008; Strand et al. 2008; Linnansaari & Cunjak 2013). Moreover, juveniles may be more active under surface ice, than during more unstable periods with sub-surface ice and/or in steep channels with more dynamic ice formation (Linnansaari, Cunjak

& Newbury 2008; Stickler et al. 2008a; Linnansaari & Cunjak 2013; Watz et al. 2015). Activity patterns may also change with the progress of winter (Stickler et al. 2008a).

Even though salmon may feed at surprisingly low light levels (Valdimarsson & Metcalfe 1999), ambient light affect capture success in visual predators like salmon and trout, and is reduced at low light levels (Fraser & Metcalfe 1997; Valdimarsson & Metcalfe 2001) as well as at low temperatures (Watz et al. 2014). Systematic active drift feeding in winter appears to be a tenuous proposition for salmon and trout (Fig. 7), because of reduced feeding efficiency associated with low temperatures and light levels, resulting from ice cover and primarily nocturnal activity with lowered prey detection probabilities and capture success (above) (Piccolo, Frank & Hayes 2014). And this is combined with reduced drift/low feeding resource biomass during the winter season (Brittain & Eikeland 1988; Matthaei, Werthmuller & Frutiger 1998; Martin et al. 2001), and possibly also under ice (Bogatov & Astakhov 2011). However, opportunistic feeding tends to remain (Fig. 7) (Metcalfe, Fraser & Burns 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 & 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 7). Such habitats may represent important winter refuges (Huusko et al. 2007; Stickler et al. 2008b).

Higher benthic macroinvertebrate abundance in winter may result from increased input of allochthonous 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 regulated rivers in winter are likely to increase benthic invertebrate production (Raddum & Fjellheim 1993): Invertebrate growth is temperature dependent, but continue 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; Bruno et al. 2009; Bruno et al. 2013; Miller & Judson 2014)

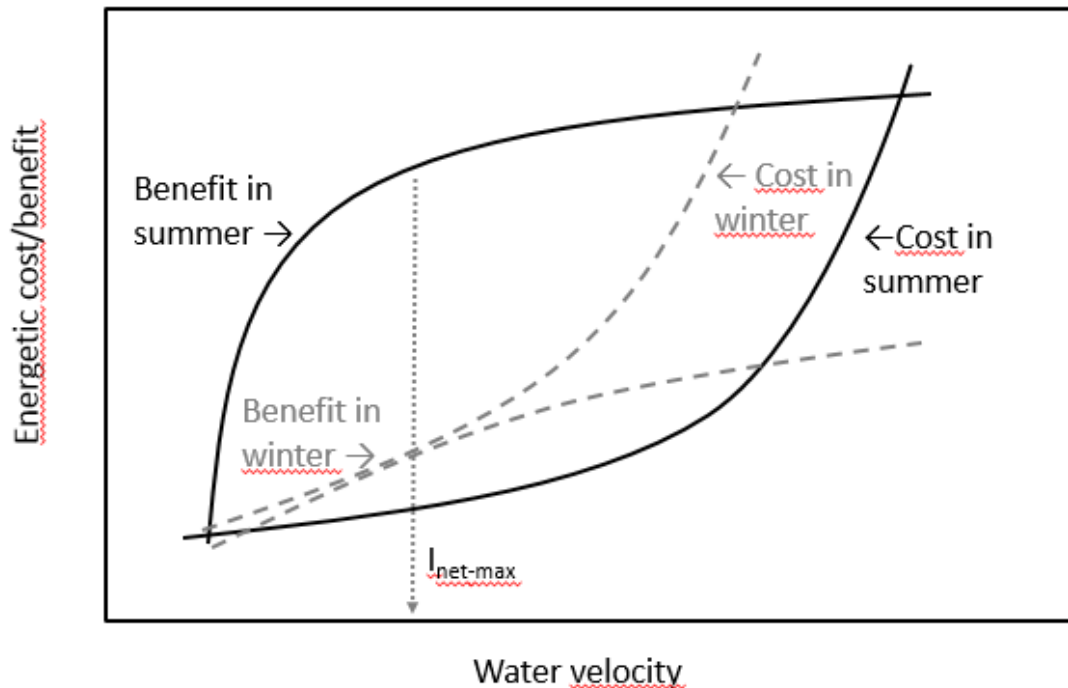


Figure 7. A conceptual cost-benefit model for drift-feeding salmonids in habitats with low perceived predation risk, in summer (solid lines) and in winter (dashed lines). Dotted line represent maximum net energy gain. In winter, reduced drift availability and capture success and increased cost will reduce or eliminate the net energy gain potential (dotted curves). The relative benefit from benthic feeding may increase in winter.

There appears to be local adaptations with respect to feeding and growth. 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). Thus northern populations appear to be adapted to the longer and more intense winters. The more cold-adapted Arctic char is in turn more successful than trout in feeding and growing at low temperatures (Larsson et al. 2005; Amundsen & Knudsen 2009; Finstad et al. 2011) and maintaining a positive energy balance during winter (Helland et al. 2011). But even Arctic char show remarkably slow growth under prolonged winter conditions (e.g. Borgstrom, Isdahl & Svenning 2015).

In response to experimentally simulated surface ice cover in semi-natural stream channels, both brown trout and Atlantic salmon may reduce resting metabolic rate and stress responses under cover (Finstad et al. 2004a; Watz & Piccolo 2011; Watz et al. 2015). They may be more active under surface ice and with a higher food intake in the experimental environments (Finstad et al. 2004a; Finstad & Forseth 2006; Watz & Piccolo 2011), although 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 (River Alta; Johansen et al. 2010; Hedger et al. 2013a). It may stem from reduced energy loss (lower stress, metabolic rate) and predation risk, possibly with more feeding when perceived risk is reduced (Finstad et al. 2004a). Higher metabolism in ice-free areas may not be offset by higher energy intake, because of similarly low prey densities in ice covered and uncovered habitats (Johansen et al. 2010). However, results are ambiguous. Other field studies have not indicated any reduced survival associated with varying surface ice cover (Huusko et al. 2007; Stickler et al. 2008a). Winter survival depends, in addition to energy reserves and risk, on the complex interplay of local habitat factors, as for example availability of substrate shelter, which may override or mask any factorial effects of surface ice alone (Huusko et al. 2007; Stickler et al. 2008b).

After a fall-early winter transition period with first pre-ice and then sub-surface ice, the second mid-winter more stable surface ice period, and as spring is approaching, usually means that juveniles tend to move more (Stickler et al. 2008a; Linnansaari et al. 2009; Linnansaari & Cunjak 2013).

Ice breakup is the final major habitat-hydraulic change in the winter ecology of a stream (Scrimgeour et al. 1994). In regulated rivers mechanistic ice breakup may occur several and anytime during winter. Mechanistic ice breakup events with their associated physical disturbance effects may certainly cause very high mortalities, both in eggs and parr (Cunjak, Linnansaari & Caissie 2013). Unfortunately, few other winter mortality studies are, however, 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). Mechanistic ice breakup events is a likely candidate to cause high winter mortalities, but this remains largely to be documented.

5.2. Water flows

River flow regimes in general have fundamental effects on riverine ecosystems and their salmonid fish populations through influencing key processes and factors like temperature, drift, dissolved oxygen, water quality, sediment scouring, transport and deposition, and habitat availability, type and distribution (e.g. Armstrong & Nislow 2012; Warren, Dunbar & Smith 2015). Because salmonids often exhibit major changes in habitat requirements during their life cycle, effects of changes in flow tend to be highly stage-specific. Modelling (empirical, process based) input of water flow and output of characteristics of fish, such as survival and growth, suggests that flow-related gains or losses early in ontogeny are particularly important in salmon and trout (Malcolm et al. 2012; Nislow & Armstrong 2012; Cunjak, Linnansaari & Caissie 2013). Based on empirical and process-based modelling, a conceptual dome-shaped model is suggested for the relationship water flow and fish 'production' (which may be expressed by different variables relevant to the population, e.g. number and size of individuals at various life stages) (Fig. 8) (Armstrong & Nislow 2012). The basic assumptions are that production will approach zero at both low and high discharges (water is needed to produce, and high water may displace fish, make feeding impossible and induce bed scour). Between those limits, production is likely to peak at some (range) discharge level at some critical component of the life cycle. This simplistic conceptual model will be modified by the physical structure of (habitat provided by) the relevant river reach, and in combination with fish life stage. Often full wetted width is considered to be a *critical low flow threshold*. Management models are currently in use that focus on specific low flow cut-off levels, specifically Q₉₅, presumably critical to fish production, and reflecting a discontinuity (maximum curvature) in the flow-wetted area relationship (Fig. 8) (below) (Gippel & Stewardson 1998; Booker & Acreman 2007). This is a simplistic empirical-based model implicitly assuming that wetted width will drop sharply below Q₉₅. It will, however, be modified by stream physical structure. Basically, in the more common U-shaped form, wetted area will drop sharply below a threshold flow, which may coincide with Q₉₅. However, in a V-shaped channel form, wetted width varies linearly with flow, and no critical flow can be identified (Fig. 8). Furthermore, this basic pattern will be modified by flow-dependent, but likely non-linear changes in water depths and velocities (whereas substrates may change less with increasing flow) (Fig. 8), which are also important habitat factors for trout and salmon (e.g. Heggenes, Bagliniere & Cunjak 1999; Armstrong et al. 2003; Klemetsen et al. 2003). Furthermore, this conceptual model does not consider timing or variation in, or frequency and duration of flows. They will have different effects on the different life stages of

salmon and trout (spawning, eggs, larvae, juveniles and adult), in particular early in ontogeny (e.g. Young, Cech & Thompson 2011; Nislow & Armstrong 2012; Warren, Dunbar & Smith 2015).

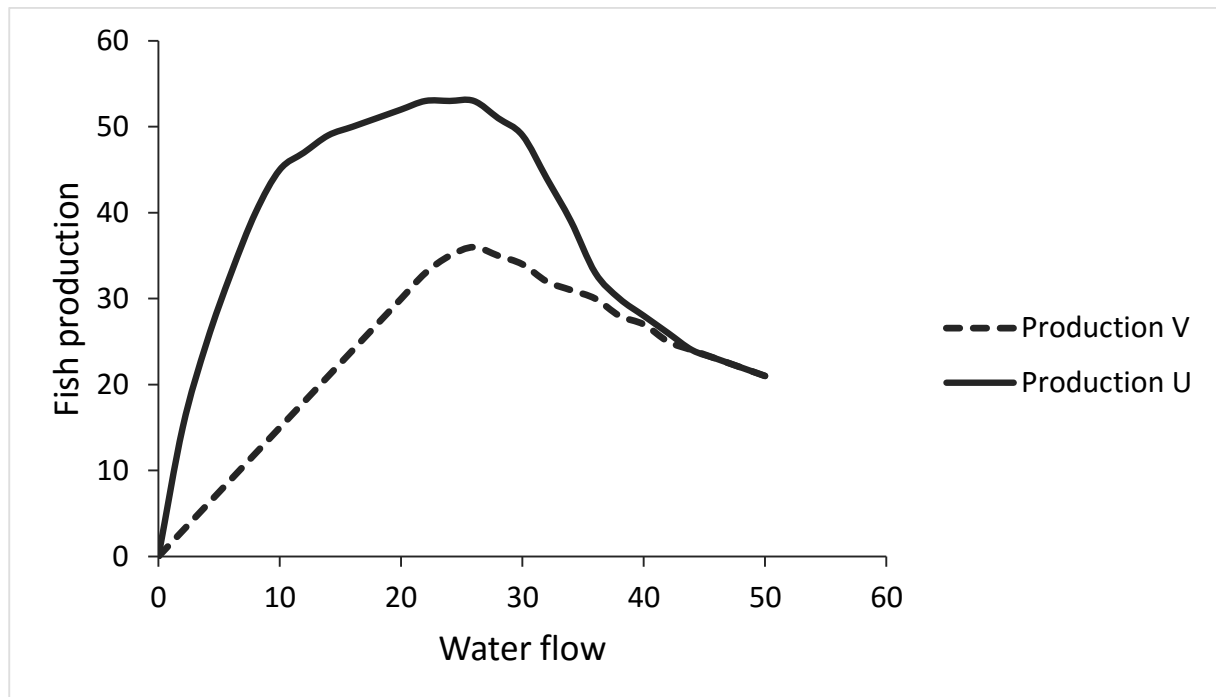


Figure 8. Conceptual model of relationship between water flow and salmonid fish production for a V-shaped (dotted line) vs. U-shaped (solid line) river bed. The environmental minimum flow illustrates a point at which a target production occurs (preferably near maximum). The flow at which a potential wetted-width nick point occurs (sometimes referred to as Q_{95}) indicates dramatically increasing production loss. Such a point will depend on river bed morphology and hyporheic volume. In a V-shaped river bed (dotted line), there may not be a nick point. In the more common U-shaped river bed (solid line), habitat availability will decrease disproportionately when flow drops below wetted width.

5.3. Low flows, natural and regulated

If flows are diverted for example by hydropower production, and reduced environmental flows are set downstream, the conceptual model indicates a loss in production. However, the magnitude will obviously depend critically on the in situ flow-production curve, of which we rarely have sufficient data. For example, (natural) high flow events may be of little importance to salmonid production (George et al. 2015), whereas low flow events may for obvious reasons be critical (Elliott, Hurley & Elliott 1997; Warren, Dunbar & Smith 2015). Low flows means reduced habitat quality, i.e. stream depths and velocities, increased sedimentation, changed thermal regime and water chemistry, and

possibly reduced habitat quantity and connectivity, i.e. width and available wetted area resulting in elevated fish densities. Preferred feeding habitats may be reduced or not available, whereas the effect on the benthic invertebrate food base usually is changed species composition and reduced richness, but not necessarily abundance (Dewson, James & Death 2007). Increased fish densities combined with low flows may present higher risk of hypoxia and predation, including cannibalism (Heggenes & Borgstrom 1988; Smith & Reay 1991; Vik, Borgstrom & Skaala 2001; Portz, Woodley & Cech 2006), and reduced feeding and growth (e.g. Stradmeyer et al. 2008; Brockmark, Adriaenssens & Johnsson 2010; Reid, Armstrong & Metcalfe 2011)), resulting in increased mortality (Elliott, Hurley & Elliott 1997; Elliott 2006). Injuries associated with increased aggression, and transmission of pathogens, may also contribute. If flow is reduced below a potential critical wetted width threshold (above, Fig. 8) the habitat starts to fragment, and isolation and increased risk of stranding become a threat (Hunter 1992; Halleraker et al. 2003; Young, Cech & Thompson 2011). It can result in oxygen and temperature stress (Elliott 2000), and desiccation, predation and mortality on fish eggs, fry, juveniles and sometimes adult salmonids. This may depend on fish, habitat and flow characteristics. In regulated streams important factors are fish size and species, 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). 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 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 disrupting habitat connectivity will obviously also disrupt non-local movements and migrations, e.g. for feeding and spawning which may affect production through reduced survival, growth and recruitment.

Low flow interact with temperature. In summer, higher temperatures will exacerbate 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).

Consequently, studies have found that low flows, e.g. during summer (Elliott, Hurley & Elliott 1997; Bell, Elliott & Moore 2000; Hvidsten et al. 2015b) 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. 2015b). Restored/increased flows in regulated rivers have resulted in higher salmonid production (Sabaton et al. 2008). Higher minimum discharge in winter after regulation, may improve parr survival rates and subsequent smolt production (Hvidsten et al. 2015b). Sudden drops in water discharge, associated with hydropower regulation, result in increased salmon and trout mortality because of stranding (Saltveit et al. 2001; Halleraker et al. 2003), and should be avoided. 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 (below) may increase juvenile fish survival (Johnsen et al. 2011; Hedger et al. 2013a).

Low flows during winter that lead to dry conditions and subsequent freezing of the riverbed, will significantly 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).

5.4. High winter flows

High flows may initially increase available habitat, e.g. side channels and floodplain areas (Junk, Bayley & Sparks 1989) and benefit egg and juvenile winter survival in streams (Frenette et al. 1984; Cunjak, Linnansaari & Caissie 2013; Hvidsten et al. 2015b), and also provide nutrient input through flushing (Bowes, Leach & House 2005). However, similar to low flows, in situ effects will depend on fish, habitat and flow characteristics (above). Water flow (variations) may have a timer effect e.g. for spawning migrations (Tetzlaff et al. 2005). Atlantic salmon and brown trout need sufficiently high flows to reach their spawning areas (Cunjak, Linnansaari & Caissie 2013). They then carefully select spawning sites that tend to be resilient to environmental changes, based on substrate particle size, water depth and velocities (Crisp & Carling 1989; Louhi, Maki-Petays & Erkinaro 2008; Wollebaek,

Thue & Heggenes 2008). The non-mobile egg stage depend entirely on local physical conditions during winter. Eggs in the substrate may be damaged and lost if flows occur that are high enough to mobilize spawning substrates (Jensen & Johnsen 1999). The relatively short emergence and alevin phase (newly hatched but still attached to the yolk sac) is primarily regulated by temperature (Elliott & Hurley 1998a; Elliott 2009; Cunjak, Linnansaari & Caissie 2013), but spawning date may influence length of emergence period (Elliott & Hurley 1998a). The emergence phase is particularly sensitive with respect to environmental conditions, including flow, and often considered critical. Alevins and then young larvae have limited swimming capacity and drift downstream for dispersal which confers energetic benefits (Einum et al. 2011), and maybe in adaptive synchrony with small discharge events (Cunjak, Linnansaari & Caissie 2013). They may, however, also be vulnerable 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 moribund (Elliott 1994). Thus high water velocities may reduce brown trout recruitment, e.g. below dams (Dibble et al. 2015) Their ability to swim and maintain position by seeking out low-velocity micro-niches in the water column (Heggenes, Bagliniere & Cunjak 1999; Heggenes 2002; Armstrong et al. 2003) improves rapidly with body size (Heggenes 1988), suggesting that the impact of high flows may be limited. Conversely, in the absence of floods, larvae and juveniles may not be redistributed, resulting in elevated densities and associated negative competitive effects (Einum et al. 2008; Einum et al. 2011). High flows during later life stages appear to have limited direct negative effects on trout and salmon (George et al. 2015), except perhaps in the more extreme cases when debris and substrates are mobilized (Sato 2006; Vincenzi et al. 2012). Also, within a restricted river channel, increasingly high flows with associated high water velocities, will reduce available habitat and increase energy cost associated with feeding and holding position (Hill & Grossman 1993; Kemp, Gilvear & Armstrong 2006; Grossman 2014).

High flows in winter providing more habitat, may be beneficial for salmonid survival and production (Cunjak, Prowse & Parrish 1998; Cunjak, Linnansaari & Caissie 2013). Winter high flows may also trigger more activity and movement, in particular high flows during spring ice breakup (Brown, Power & Beltaos 2001).

As noted, hydro-peaked systems tend to aggravate high-low flow effects, depending on down-ramping rate, ramping amplitude, frequency of flow fluctuations, prior flow conditions, timing of pulse (see Young, Cech & Thompson 2011 for reviews; Rolls, Leigh & Sheldon 2012; Ellis & Jones 2013; Warren, Dunbar & Smith 2015). Beneficial ecological effects, depending on management regime, may include resource subsidies from upstream reservoir (Ellis & Jones 2013), maintenance of habitat for spawning and rearing, and biological cues to trigger spawning, hatching and migration (Young, Cech & Thompson 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 red dewatering (above; Young, Cech & Thompson 2011).

5.5. Fish migrations and spawning

The local movements between daytime refuges and night-time slow-current activity areas (Rimmer, Paim & Saunders 1984; Cunjak, Power & Barton 1986; Heggenes et al. 1993), result only in very little movement on a diurnal basis, maybe less than 1m, but with individual variation (Stickler et al. 2008a; Linnansaari & Cunjak 2013). Larger fish, and even juveniles, may also move more extensive distances (Linnansaari et al. 2009) to find more restricted suitable deep-slow refuge habitats where they may aggregate (Brown, Stanislawski & Mackay 1994; Brown 1999; Saraniemi, Huusko & Tahkola 2008).. As surface ice cover increases and also spring approaches, fish may become more active and move more (Stickler et al. 2008a; Linnansaari & Cunjak 2013).

For upstream spawning and downstream 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. Particularly in smaller streams, water flow may control when the spawners enter rivers, and antecedent and current flow, flow variations, and temperature the timing of the ascent, 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). Thus the more exact timing of spawning migration will be site and population specific, depending on when the long-term migratory opportunities to reach their spawning areas, are best (Jonsson & Jonsson 2009; Cunjak, Linnansaari & Caissie 2013), but modified by anthropogenic impacts (Thorstad et al. 2008; Milner, Solomon & Smith 2012). An expected consequence is that if flows are consistently high, e.g. in wet

years, or rivers large, flows and/or variations may not influence ascent directly, whereas this may be important in dry years (Tetzlaff et al. 2008), and low flow may limit length of upstream migration. On the finest temporal scale, flow will dictate which suitable stream areas (e.g. Louhi, Maki-Petays & Erkinaro 2008) are available for spawning. In natural northern systems this will tend to be at relatively high discharges, in particular for fish spawning in the upper parts of a system (Gibbins et al. 2002; Malcolm et al. 2012). Locally different hydraulic geometries of spawning areas, may explain spatial differences in suitable discharge (Sear & DeVries 2008; Malcolm et al. 2012). In regulated systems, flow during spawning season should not be higher than minimum maintained flow during winter to avoid dewatering (Casas-Mulet et al. 2015; Casas-Mulet, Saltveit & Alfredsen 2015). There is little knowledge as to how flow variations per se may influence spawning.

During autumn spawning salmon and trout typically bury their egg 10-30cm into river gravels, depending on species and fish size, and substrate particle size (de Gaudemar, Schroder & Beall 2000; Louhi, Maki-Petays & Erkinaro 2008; , but see Riedl & Peter 2013), It is likely also a trade-of between scour depth and water quality which 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 (~1-6°C for peak spawning) (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.

5.6. Egg incubation and embryonic development

The spawning time-temperature link arises from the fact that the duration of embryonic development primarily depends on number of day-degrees from spawning to hatching (Elliott & Hurley 1998c). 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 (Elliott 1994). On the individual and population level, if emergence is either too early or too late, survival will be reduced (Einum & 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).

The time between spawning and alevin emergence is important period in the life cycle of salmonids, and may impose substantial, but highly variable mortality on populations (Sear & DeVries 2008; Malcolm et al. 2012). As embryonic development is controlled by the specific numbers of day-degrees required, timing of emergence may vary greatly among years within a population, mainly because of variations in water temperature, 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 (heat-sum) required from fertilization to emergence may show little adaptive variation among natural Atlantic salmon populations (Heggberget & Wallace 1984; Wallace & Heggberget 1988), but studies are limited with respect to population gradients studied and results somewhat ambiguous. There are indications that this sum may vary somewhat, and tend to be lower at low winter temperatures near 0°C and highest at an intermediate temperature (Jonsson & Jonsson 2009). Effects of incubation temperature on alevin size, also appear ambiguous, but with egg size is the major determinant (Elliott & Hurley 1998c). Egg size depends on maternal size, whereas timing of spawning does not seem important (Louhi et al. 2015).

Environmental stress, e.g. mechanical disturbance due to high flows, or low oxygen levels, may induce earlier hatching (Jonsson & Jonsson 2009), presumably as a resilience response. Eggs with embryo appear to be most tolerant for disturbance (Becker, Neitzel & Fickeisen 1982; Neitzel & Becker 1985). However, high winter flows leading to mechanical substratum disturbance may also 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 mortalities associated with rare ice breakup events are documented (Cunjak, Linnansaari & Caissie 2013). In natural systems salmonids may perhaps have evolved to bury their eggs in relatively stable areas that do not typically experience scour (Malcolm et al. 2012) to the extent that scour events may be predictable, but this will be different in regulated systems (Tab. 5).

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). Survival depends on a range of biotic and abiotic factors (Greig, Sear & Carling 2007; Gibbins et al. 2008; Malcolm et al. 2012; Saltveit & Brabrand 2013), e.g. gravel composition, sediment transport,

temperature, groundwater influx, and water flow rates, all of which may be altered in a regulated hydraulic regime. Scouring and dewatering may be particularly important. Low flows during winter, e.g. in regulated hydropeaking rivers may lead to dewatering of salmon and trout spawning redds (Tab. 5), especially if spawning occurs at relatively high flows (Casas-Mulet, Alfredsen & Killingtveit 2014; Casas-Mulet, Saltveit & Alfredsen 2015). Although winter dewatering may lead to egg freezing and mortality (Casas-Mulet, Saltveit & Alfredsen 2015), mitigating effects of groundwater combined with local hyporheic environments and hydraulic regime confound effects, which therefore may not always be straightforward (Malcolm et al. 2012), and in situ studies may be required (Becker & Neitzel 1985; Casas-Mulet, Saltveit & Alfredsen 2015). However, 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).

5.7. Emergence and early mortality

If hydraulic conditions are stable and favorable throughout winter, egg survival is usually high (above). In contrast, 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), 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, and 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). Whereas timing of emergence is temperature dependent (above), alevin and larvae size depend on egg size, which again primarily depend on female spawner size (Elliott & Hurley 1998c; 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 (Robertsen, Skoglund & Einum 2013).

Density-independent abiotic factors such as flow, temperature and ice may be more important in regulating low-density (below carrying capacity) and populations in more challenging environments (Elliott 1989; Elliott & Hurley 1998b; Lobon-Cervia & Mortensen 2005; Cunjak, Linnansaari & Caissie

2013; Lobon-Cervia 2014). Alevins and young fry are more sensitive than eggs to environmental conditions (Neitzel & Becker 1985), e.g. dewatering and oxygen (Tab. 5). Studies indicate a positive relationship between water discharge and egg/fish survival (Tab. 5), e.g. egg and underyearling survival in Atlantic salmon (Gibson & Myers 1988; Cunjak, Linnansaari & Caissie 2013) and spring flow and brown trout survival (Carline 2006; Lobon-Cervia 2014). Extreme floods during the alevin stage may however, induce increased mortality (Elliott 1985; Jensen & Johnsen 1999). Conversely, low winter flow and ice, or spring flow at or soon after emergence, may reduce egg and/or juvenile survival (Tab. 5) (Elliott 1985; Borgstrom & Museth 2005; Cunjak, Linnansaari & Caissie 2013).

Temperature influence emergence, early feeding and survival (Tab. 5). 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). 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, and increasing with temperature. 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. Table 5 highlights some likely winter regulation effects and potential biological effects.

Table 5. Summary of winter regulation effects on flow, water temperature and ice. Question marks indicate uncertainty.

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	
	Sub-surface	Reduced and unstable habitat	Subsequent increased drift
	Breakup	More frequent, fish and egg mortality during scouring events	Subsequent increased drift

6. Integrating hydro-physical and biological knowledge

Understanding and mitigating effects of hydropower regulation on winter flow and ice is complex. Interactions between the physical system and ecological responses are complicated, and the understanding of and data availability on winter processes are limited. Nevertheless, there is a growing number of management-oriented models and methods available to also explore and tackle winter conditions. The integration of physical simulation models with models of fish responses into a holistic framework is needed and in progress. This progress is also driven by the increasingly feasible collection of extensive data for setup, validation and monitoring, based in new technology for measuring physical and biological variables. New opportunities for the future are provided by remote sensing of data by LiDAR (Legleiter et al. 2015; Mandelburger et al. 2015), thermal mapping (Dugdale, Bergeron & St-Hilaire 2015a), new methods for measuring and observing ice (Ghobrial, Loewen & Hicks 2013a; Ghobrial, Loewen & Hicks 2013b), and improved high-resolution tracking techniques for fish (e.g. Stickler et al. 2008a; Linnansaari & Cunjak 2013; Weber et al. 2016). Moreover, multi criteria decision systems aid in combining results to support decisions, in a framework with a multitude of data and knowledge.

6.1. Modelling hydro-physical and biological winter conditions in regulated streams

The winter environment in regulated rivers results from interactions among climate, power plant operation, local hydrology and river hydraulics. This is a challenging complexity for estimation of hydropower impacts and design of predictive methods for impact assessment. A suite of numerical models may be used to tentatively assess these impacts (Timalsina, Alfredsen & Killingtveit 2015). Currently, the main challenge is in modelling and understanding ice formation and ice breakup, particularly in steep rivers, but recent work on ice monitoring and model development has brought advances (Beltaos 2012) .

One-dimensional models for the simulation of river ice has evolved over the last decades (Shen, Wang & Lal 1995; Shen 2010) into useful tools for simulation of ice formation, transport and growth (Table 6). Most of these models (RICE, RIVICE, CRISSP1D) have focused on problem-solving related to larger-scale rivers in Canada and USA, and consequently with limited ability to handle the more small-scale

and complex variable flow conditions and hydraulics in steep streams (Bjerke & Kvambekk 1994). For larger rivers, the application of ice models for practical problem-solving have in many cases been successful. Lindenschmidt, Sydor and Carson (2012) successfully ran the RIVICE model to simulate flood levels from surface ice and frazil formation during freeze-up. Jasek et al. (2015) used the CRISSP1D (a successor to RICE; Table 6) model to compute the effect of fluctuation in flow due to formation and release of anchor ice in the Peace River. The model was used to evaluate how different effects of anchor ice formation influence stage and discharge in the river to better understand the interaction between ice formation and river hydraulics. Built on the 1D hydraulic model MIKE11 from DHI, MIKE-ICE (Theriault, Saucet & Taha 2010) has a comprehensive ice module built on the fully dynamic hydraulics in the underlying MIKE11 system. Timalsina, Charmasson and Alfredsen (2013) simulated ice formation in a relatively large regulated river (Orkla River, Central Norway) using the MIKE-ICE model, investigating how different water release strategies influenced ice production and ice cover formation. The model showed good agreement with observed types of ice, and locations where ice formed, but simulated volumes of ice are yet to be tested. Theriault and Taha (2013) used the MIKE-ICE model to simulate frazil accumulations and a hanging dam in the Romaine river system, Canada, and how ice accumulations influenced water levels at a power plant outlet. The model managed to simulate thermal erosion of accumulations, but had problems simulating breaches in hanging dams. She, Hicks and Andrishak (2012) used the River1D model to simulate a freeze-up ice consolidation event during hydro peaking operation in the Peace River in Canada. The dynamic model managed to compute an ice jam comparable to the observed jam.

The application of these 1D ice models require rather detailed data on numerous river cross sections, climate and boundary conditions for flow and temperature (Table 5). These data requirements have limited the application of ice models in many rivers. Recent advances in data measurement technologies (such as LiDAR and satellite (Lindenschmidt & Chun 2014; Legleiter et al. 2015)) and efficient field techniques reduce the extent of the fieldwork. However, additional systematic collection of ice data across years for calibration and validation is advisable. Such data are often difficult to obtain and data collection programs may be needed.

Table 6. Models developed to simulate ice formation in rivers.

Model	Characteristics	Experiences	References
RICE	1D ice model, water temperature, ice concentration, ice cover formation, under cover transport, thermal growth and decay, mechanical forces.	Rapidly varying flow can be a problem. Applied in Norway.	(Lal & Shen 1991; Bjerke & Kvambekk 1994)
CRISSP1D	Successor to RICE. Improves hydraulics, freeze-up, transport and breakup. Commercial.		(Chen, Shen & Jayasundra 2006; Jasek <i>et al.</i> 2015)
RIVICE	Dynamic 1D model. Simulates the thermal regime, ice cover formation, frazil and anchor ice, transport, hanging dams, break-up and jams.	Relatively few examples of use. Simulation of ice cover formation reported to work well.	(Lindenschmidt, Sydor & Carson 2012)
River1D	1D finite element model. Thermal, ice cover and frazil simulation. Transport and consolidation events.	Examples of use in climate studies. Used successfully to simulate consolidation events in hydro peaked rivers.	(She & Hicks 2006; Andrishak & Hicks 2008; She, Hicks & Andrishak 2012)
MIKE-ICE	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, although large anchor ice events can be a problem. Applied in Norway.	(Theriault, Saucet & Taha 2010; Theriault & Taha 2013; Timalisina, Charmasson & Alfredsen 2013)
CRISSP2D	Builds on DynaRice. Solves the Shallow water flow equations, dynamic flow with wetting and drying. Simulates frazil and anchor ice. Simulated ice consolidation. Commercial.	Comprehensive set up procedure. Some applications reported in the literature, but mostly modelling exercises. Tested in Norway.	(Liu, Li & Shen 2006; Knack & Shen 2012)
River2D	2D finite element model. Ice cover induces surface roughness for under ice simulations. Well tested for ice free conditions. No temperature simulation.	Currently without ice formation simulation, but handles an ice cover. Effective setup and simulation tool. Applied in Norway.	(Katapodis & Ghamry 2005)

Micro habitat models are commonly used in ice free (summer) conditions to combine hydraulic data with fish preference data for instream environmental impact assessment (Dunbar, Alfredsen & Harby 2011), but little work has been carried out in winter time and even less in streams with ice. Knack and Shen (2012) used the two-dimensional model DynaRice to simulate habitat conditions for brown trout during open water conditions, freeze-up and stable ice conditions. The work is one of the very few examples of a dynamic ice model combined with a micro-habitat model. Standardized (summer) preferences for brown trout were used for this work (Raleigh, Zuckerman & Nelson 1986). However,

modelling results were not controlled with field data. Like most similar studies, this was rather a modelling exercise. Katapodis and Ghamry (2005) simulated under-ice habitat with the River2D model on the large Athabasca River in Canada, and discuss calibration methods and model setup for under ice simulations. The application of 2D ice models is data intensive and therefore still limited to shorter reaches of rivers. The models need detailed geometry data for the river reach, climate data for the energy balance and discharge and water temperature for boundary conditions. Data requirements for calibration and validation of 2D models are as for the 1D models. In addition, fish habitat preferences for winter are needed, and these are not readily available (but see Maki-Petays et al. 2004). Also data on the relationship between habitat in winter and behavioral and population effects (above) need to be investigated further.

The use of meso-scale stream classification based on stream morphology has gained popularity as a much more convenient and less data intensive method to assess available habitat and effects of changes in flow and river conditions on fish populations (Parasiewicz 2007; Forseth & Harby 2014a). However, meso-habitat methods are not yet applicable to stream winter conditions with ice. The above conceptual ice model by Turcotte and Morse (2013) may form the basis for further developments. An interesting approach is presented by Lindenschmidt and Chun (2014), who applied a geo-statistical model to predict ice formation based on river morphological parameters. This could provide a link between meso-scale habitats and ice formation as a tool for larger scale assessment of ice formation. Regardless, for regulated systems more work is needed for both models to include regulation effects on the ice predictions, which are not included in the original formulations.

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. However, such hydro-ecological models have important limitations (Grimm & Railsback 2013), e.g. being based mainly on the assessment of species' needs, not individuals. Habitat evaluation methods used during data collection or analyses may vary, habitat use may be confused with habitat preference, variable interactions are rarely included, and links to population growth and survival are uncertain (Garshelis 2000; Railsback, Stauffer & Harvey 2003). Habitat preference

models may be complemented by modelling action-interaction effects on the system, as in Individual Based Model (IBMs). They attempt to model the important processes that determine survival, growth, and reproduction of individual fish, including competition and habitat effects, and temporal variation (Railsback, Stauffer & Harvey 2003; Railsback et al. 2013). The IBM for Atlantic salmon in Norway called IBsalmon (Hedger et al. 2013b) offers a potential tool to quantify how abiotic and biotic characteristics affect the individuals of a specific population (Hedger et al. 2013a; Hedger et al. 2013b). 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.

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 of course that habitat is an important regulating factor. This may often be the case, but not necessarily. Jager et al. (1997) used an Individual Based Model (IBM) instead of habitat preference model, to predict instream flow effects on smolt production for fall chinook salmon (*Oncorhynchus tshawytscha*) in regulated rivers. The predictions for ontological development, growth and survival fit well with empirical studies, and indicated that flow related egg mortality in redds, and temperature related juvenile mortality, were the major limitations for smolt production, and not fish habitat per se.

A method which is seeing considerable use in describing effects of impacts of hydropower alterations on flow regimes, is the index of hydrologic alteration, IHA (Richter et al. 1996), and similar methods to evaluate hydrological variability (Olden & Poff 2003; Bevelhimer, McManamay & O'Connor 2014). This is based on the understanding that flow variability is important in maintaining the ecosystem (Poff & Zimmerman 2010). For ice free winter conditions, the indexes of variability are useful to describe flow effects previously discussed. However, from studies on ice effects on flow regimes it is known that ice formation will influence both the discharge variation through retention at freeze-up (Turcotte, Morse & Anctil 2014), and also influence other flow related variables like depth, velocity and water covered area even when there is no corresponding flow event (Stickler et al. 2010a). In the latter cases, indexes such as the IHA are unlikely to provide the data needed to understand the in-

stream conditions. Consequently, Peters, Monk and Baird (2013) developed the Cold Regions Hydrological Indicators of Change (CHIC) which takes into account several ice driven events and adds to the range of indicators in the IHA. Based on data from larger rivers in Canada, the new set of indices handles ice cover effects, break-up effects and magnitude of ice-influenced flow. Again, for smaller and steeper rivers with frequent anchor ice events, and also in rivers where hydropower drives frazil production, there is a need for further work on streamflow indices.

All the tools for ice simulation (above) will also simulate water temperature during ice-free conditions. In addition, there are several other numerical hydraulic models that have the capacity to simulate water temperature, e.g. the well-known HEC-RAS model (Jensen & Lowney 2004) or the SNTMP model (Bartholow 1991). These models require detailed description of the river system and data to describe the heat balance of the river system. A simpler alternative is to use a simplified energy balance model (Toffolm & Piccolroaz 2015), or a semi-statistical model for stream temperature (Benyahya et al. 2007). A challenge for these river temperature models is the need to provide the boundary temperature (i.e. indicating thermodynamic changes) for the simulation, if measurements are not in place. Boundary temperature is important in the simulation of river water temperature downstream of a water outlet. For a regulated system simulated temperature through the turbine from a reservoir model can be used as input (Gebre, Boissy & Alfredsen 2014), but such data are less common for catchment temperature. A possible solution is to use a hydrological model with the ability to simulate water temperature (Loiniz et al. 2013). With proper boundary conditions, such models may deliver good estimates of water temperature in downstream reaches (Toffolon & Piccolroaz 2015; Bakken, King & Alfredsen 2016)

The classification of temperature regimes in line with discharge regimes (e.g. Richter et al. 1996; Bevelhimer, McManamay & O'Connor 2014) is complicated due to a general lack of water temperature data, and in particular data for the pre-regulation conditions may not be available (Olden & Naiman 2010a). Application of water temperature classification methods over many regulated system will therefore, require temperature models with their data needs and complexities as outlined above. Olden and Naiman (2010a) shows an example of a classification using the same principles as in the IHA method for data for the Flaming Gorge Dam in the US, showing clear changes in magnitude, timing and frequency of temperature pre- and post-dam development. Another

example of a temperature classification is given by Vanzo et al. (2015), who developed indexes to evaluate sub-daily temperature fluctuations to classify river temperature regimes according to natural or altered state. The indicator manage to capture the different river types well.

6.2. Hydropower operational decisions: Integrating hydro-ecology with socio-economy

For management decisions, hydro-ecological models need to be expanded to 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 (Jager & Smith 2008; Niu & Insley 2013). Balancing the often competing demands of hydropower production and environmental protection has become increasingly important Nordic countries (Renöfält, Jansson & Nilsson 2010; Erkinaro et al. 2011; Forseth & Harby 2014a). This trend is partly driven by the implementation of more restrictive environmental laws as The European Water Framework Directive (WFD) (2000/60/EC), which, while highlighting the need to implement mitigation measures, relies heavily on the use of modelling tools for integrative methods that also include economic aspects.

The inclusion of economic aspects into integrated models for hydropower operational scenarios and decisions is not trivial. In the hydropower sector, cost estimation of market value benefits, such as flood control, water supply, irrigation, and river navigation, are relatively easy to calculate. Cost-benefit studies can also include costs for different operational strategies, to find the alternative with the greatest economic benefits to the society and/or stakeholders (Hanley, Barbier & Barbier 2009). In order to attempt to include the more evasive non-market values into the cost-benefit analyses, some studies use an indicator of the ecological status. That can be for example fish production and recreational fishing.

Kotchen et al. (2006), in developing a cost-benefit analyses of a hydropower regulation project that involved managing releases to change a peaking operational system to a run-off river, included the benefits from reduction in greenhouse gas emission from the use of thermal electricity, e.g. coal, and the benefits from an increase in the recreational fishing. They concluded that the benefits of changing the operational system of the regulated system produced higher benefits than costs. In contrast, Person et al. (2014), implementing a cost-benefit evaluation for potential mitigation measures in a hydropeaked river, concluded that changes in the operational system such as limiting maximum

turbine discharge, increasing the residual flow, and limiting the drawdown range, had a high cost in relation to their ecological benefit. Ecological benefit was expressed as 'fish response', using the CASiMiR model combined with regional univariate preference curves for adult, YOY and spawning brown trout. The most cost-effective measure appeared to be use of compensation basins rather than changing the operational system.

In Norway, a recent screening that prioritize hydropower relicensing, includes the simple minimum flow Q95 as a standard mitigation measure. The easily estimated total power loss relative to no concession restrictions is 2.3-3.6 TWh/year, corresponding to 1.8-2.8% of the median national annual power production (Sørensen et al. 2013). The ecological benefit is intuitively obvious, but very complicated, resource demanding and time consuming to quantify *in natura*. Such decision processes could benefit from more simplistic modeling approaches. However, all these models also tend to include high uncertainty. It may stem e.g. from potential climate change, biological complexity and variability, and unpredictable market prices, which generate complex and dynamic nonlinear processes and spatial and temporal lags (Costanza & Ruth 1998; Brown et al. 2015). Still, the integrated use of different models may develop alternative scenarios, and perhaps anticipate those dynamics based on available data and knowledge, and possibly develop consensus decisions (Costanza & Ruth 1998).

A key is always to make the relevant scientific information accessible and understandable for the decision makers with an effective communication (Liu et al. 2008). The strength is the output from an integrated modelling approach, which is structured and predictable results. This may form the basis for decisions promoting sustainable management in river ecosystems (King et al., 2003).

Over the last decades, the application of so-called Multi-Criteria Decision Analysis (MCDA) in different areas has increased significantly. Velasquez and Hester (2013) summarized different related methods used in water management (e.g. Multi-Attribute Utility Theory, Goal Programming, ELECTRE, PROMETHEE, Simple Additive Weighting, Technique for Order of Preference by Similarity to Ideal Solution) to evaluate trade-offs associated with alternative river management. These methods allow prioritizing among different management options, and can incorporate social preferences in the prioritization process (Martin, Labadie & Poff 2015). MCDA methods can be used to support environmental decisions in traditional management schemes, but their strength is when

they are coupled with adaptive management (Figure 9) (Walters 1986; Linkov et al. 2006). MCDA have the potential to include the implicit trade-off from in environmental cost-effective analyses (Karjalainen et al. 2013).

Still, their implementation has been limited to a few long-term projects in natural resources with a high level of uncertainty. According to a recent review (Karjalainen et al. 2013) only Proctor and Drechsler (2006) and Oikonomou, Dimitrakopoulos and Troumbis (2011) have combined the multi-criteria evaluation techniques with the ecosystem services framework. Unfortunately, these cases were not part of environmental impact assessment processes. An important difficulty is the inclusion of ecological benefits (Karjalainen et al. 2013), often referred to as ecosystem services (ES), i.e. the social benefit obtained from ecosystems, and interactions between ecosystems and human wellbeing (Daily 1997). Problems arise from the stakeholder's distant way of thinking about the ES, and the neglect of the trade-offs (Karjalainen et al. 2013; Böck et al. 2015)

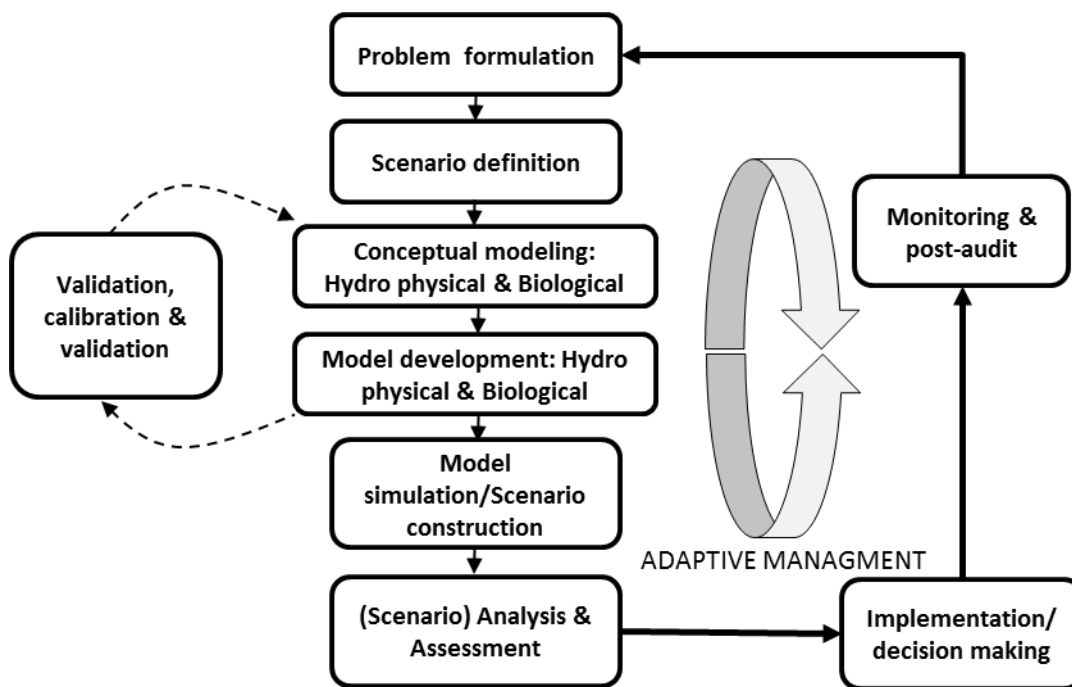


Figure 9. Integrative method framework for effective decision support through integrated modeling and scenario analysis. An example of a MCDA method. Modified from (Liu et al. 2008).

MCDA has additional limitations. Social preferences cannot be included directly as nominal, qualitative variables, only as quantitative variables. Furthermore, it is difficult for stakeholders and decision makers to understand the method due their complex structure (Myllyviita et al. 2011). Fenton and Neil (2001) argued that MCDA usually use methods that focus on decisions under certainty, and therefore, uncertainties among interactions and among criteria are not modelled in a coherent and systematic manner.

To improve the MCDA, Fenton and Neil (2001) proposed a decision framework based on Bayesian Networks (BN) and Influence Diagrams (ID) to structure and manage the MCDA and include uncertainties into the model. Bayesian networks are probabilistic graphical models that represent a set of variables and their conditional interdependencies (see also Bromley et al. 2002; Acreman 2005). Barton et al. (2012) promote the use of BN to handle water resource management, since BN have had progress in computational methods, best practices for model design, and model communication, and are able to deal with uncertainties. However, we are not yet aware of projects

that have included BN for decision making to manage, in an integrative way, water resources in Northern Europe.

New software such as HUGIN (Hugin 2014) that is based on Bayesian Networks, provide graphical models, Bayesian Decision Network (Figure 10), that structure knowledge about a decision problem into a map of causes and effects between key variables. These BN graphical systems can be used to support stakeholder engagement, common dialogue, and communication between stakeholders, authorities, and researcher communities. This Bayesian Decision Network may indicate optimum decision pathways that minimize costs, maximize benefits or solve some other desired outcomes (Pollino & Henderson 2010). Figure 10 also shows how Bayesian Decision Network could be coupled with the MCDA framework in the implementation/decision making' box from Figure 9.

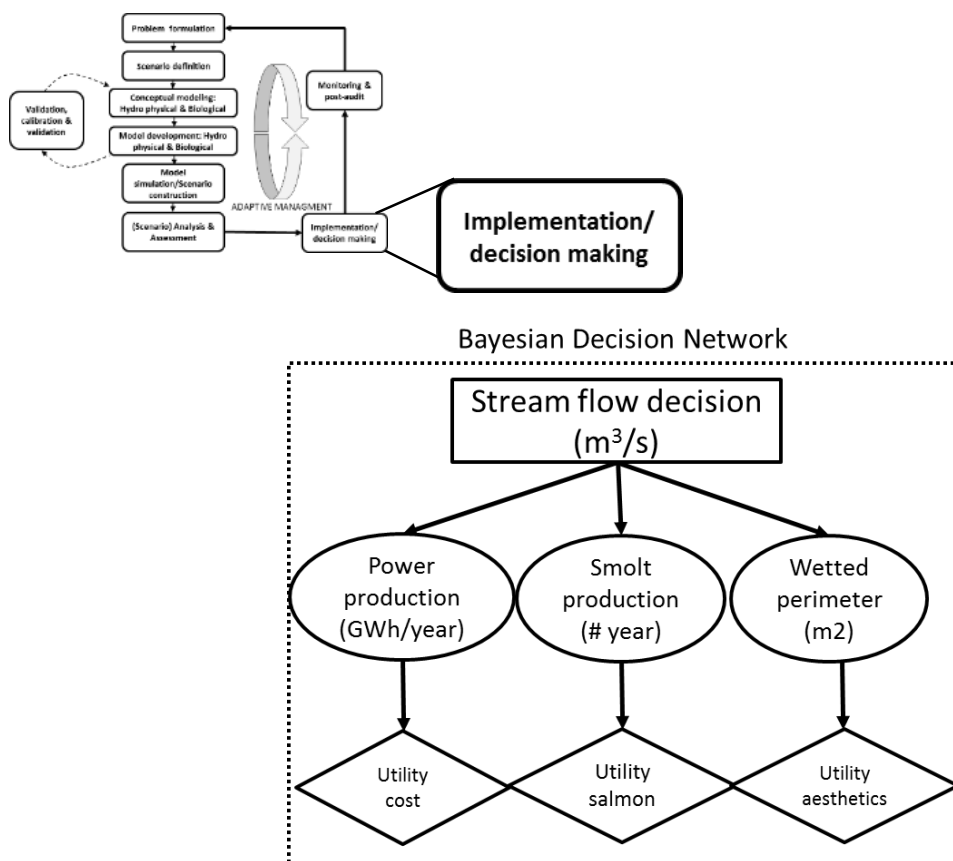


Figure 10. Bayesian Decision Network based on Barton et al. (2008) showing a case example for change in water releases in a regulated river.

6.3. Mitigating issues

In cases where the natural *water temperature* is changed by hydropower impacts, physical mitigation measures such as flexible water release strategies, and/or methods for mixing water from different sources, can be applied (Table 7) (Forseth & Harby 2014b). The first technique is useful to solve problems related to both warm and cold water changes, whereas the second is primarily useful for cold water problems (Sherman 2000). The mitigation measure 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 11) (Olden & Naiman 2010b). The effectiveness of this mitigation measure for flexible control of downstream temperatures for defined ecological goals, is well documented (Olden & Naiman 2010b). 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. In Norway, the use of this measure with the aim to increase and stabilize surface ice cover, has proved successful (Table 7) (Johnsen et al. 2010). Alternative measures to multi-level reservoir intakes for restoring ice surface cover, may be difficult to find.

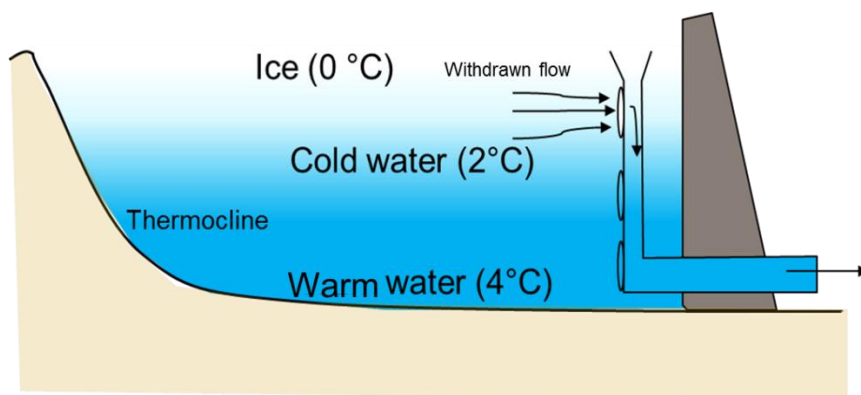


Figure 11. Multi-level intake structure that makes use of the stratification within the reservoir by permitting water with desirable thermal attributes (in this case winter condition, therefore upper layer) to be withdrawn from defined regions within the water column. Modified from Sherman (2000).

Maintaining a *minimum environmental flow* is probably the most common mitigation measure applied to hydropower regulations, e.g. the low flow index Q95 (Table 7) (Bakken et al. 2012). The Q95 is simple, but has a biological rationale (above), although rarely quantified. It is the flow value that is exceeded 95 % of the time. A minimum flow secures a crucial minimum of ecological habitat, continuity and connectivity in space and time. It's attractive simplicity make it one of the most

common methods for defining a flow target, based on simple hydrological indices (Tharme 2003; Clifford, Acreman & Booker 2008; Gopal 2013). However, many studies have reported that this methodology is highly inadequate in terms of meeting more specified environmental requirements (McClain & Anderson 2015).

Q95 is usually calculated across the year, as a flat and invariable index. In northern catchments it may be close to natural minimum flow in winter (when precipitation is stored as snow), but the Q95 calculated will rarely fulfil the ecological requirements in summer (Bakken et al. 2012). Engeland and Hisdal (2009) suggest the alternative approach to calculate the seasonal flow percentiles. Still, a seasonally variable index do not consider the dynamics and variation in the natural flow regime of the river. This is an important ecological factor per se (Poff et al. 2006). New ecohydrological models have been developed that also attempt consider species water flow needs and/or ecological functions, e.g. the Building Block Method (BBM) (King et al. 2000). In Norway Alfredsen et al. (2012) recommend the use of BBM for defining environmental flows in regulated rivers. This method is more data demanding than the Q95, and knowledge of interactions between ecological and hydrological processes is needed. Together with additional reasons like the reduction of water availability for well-established economic water uses (e.g. hydropower), it makes improved practices in environmental flow settings a challenging enterprise.

River regulations generating higher water discharges in winter, with associated higher water temperatures, have in some cases resulted in a higher smolt production (Table 7) (Hvidsten 1993; Ugedal et al. 2008b). The confounding effects of temperature and changed ice regime are difficult to disentangle (Table 7).

Hydropeaking is an unnatural and challenging flow regime for stream organisms. A minimum flow will create a refuge for macroinvertebrates and fish during the up- and down-ramping of water flow. Stranding of fish, and presumably also invertebrates, will depend on pulsed flow regime, e.g. amplitude, frequency, and rate, which preferably all should be reduced (Table 7) (Saltveit et al. 2001; Halleraker et al. 2003). Timing is important, and dewatering at night when fish are more active, particularly at low temperatures will reduce juvenile stranding (Saltveit et al. 2001; Halleraker et al. 2003). In-stream measures like construction of groundsills or weirs, groins, stone settings, river bed

adjustments, and digging of pools have been reported as useful measures (Charmasson & Zinke 2011). These measures are similar to measures designed to improve fish habitat and the ecological status of rivers in general, and therefore serve two purposes (Charmasson & Zinke 2011).

Mitigation measures to reduce ice impacts on hydropower operations are common, and include operational restrictions, ice control devices, specific winter design guidelines and thermal control measures (Wigle et al. 1990; Gebre et al. 2013). Some operational measures like aiming at developing an ice cover to prevent super cooling and frazil production via flexible reservoir intakes, will also restore near-natural conditions and benefit aquatic organisms and ecological processes. Other operational or structural measures like ice breaking and blasting and changes to the river by dredging and plastering may exacerbate negative regulation effects.

7. Conclusions and future research

The challenging physical conditions during the cold northern winters is a natural bottleneck for most organisms living in those environments, including streams. It is the season for tolerance, quiescence, starvation, and survival. Survival in streams may depend on a delicate and complex balance between winter intensity and duration, generated ice phenomena, and the organisms' energy stores, physiological adaptations, and local, habitat-dependent behavioral adjustments. Hydropower regulation may alter this natural environment in complex ways, but usually via increased downstream water temperatures, reduced surface and increased sub-surface ice formation, and increased downstream water flows. Pulsed flow regimes are a particular challenge, depending on amplitude, ramping rate, frequency, timing, and prior flow, and are difficult to generalize.

These hydropower regulation effects all directly affect stream habitat, generating a variety of biological responses discussed more in detail above. Table 7 gives a brief overview summary of considerations regarding biological and physical impacts from hydropower. In conclusion, winter is the understudied season in running waters (Huusko et al. 2007; Beltaos & Prowse 2009; Gebre et al. 2013), and for the very same hostile seasonal reasons that challenge fish survival. In a shorthand table and pointed list of research topics, we sum up the more detailed review above.

Table 7. Design and operation of hydropower installations (temperature, flow, intake, outlet) to increase performance of salmon and trout. 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.

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	**	Flexible reservoir intake	***
			Increased compensatory feeding activity?	*		*
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?	***

<i>Ice breakup</i>	<i>Increased frequency and intensity</i>	<i>Scouring, floods</i>	<i>Reduced survival</i>	<i>***</i>	<i>Flow regulation ?</i>	<i>*</i>
<i>High flow</i>	<i>Increased level and duration downstream</i>	<i>Increased habitat volume</i>	<i>Increased survival?</i>	<i>**</i>	<i>Stable higher flows</i>	<i>***</i>
<i>Low flow</i>	<i>Reduced level and increased duration in by-pass sections</i>	<i>Reduced habitat quantity, quality, connectivity, increased ice formation</i>	<i>Reduced survival</i>	<i>**</i>	<i>Stable and high minimum flow</i>	<i>***</i>
<i>Pulsed flow</i>	<i>Variable</i>	<i>Bottlenecked by low flows</i>	<i>Reduced survival</i>	<i>**</i>	<i>Reduced amplitude, ramping rate, and frequency</i>	<i>**</i>

Suggested future research needs (see text above for details):

Regulation effects on physical conditions

- Ice phenomena in steep gradient streams, in particular ice breakup
- Development of frazil ice downstream of hydropower plants
- Extent of reduced ice cover and increased frequency of ice breakups
- Downstream longitudinal thermal and ice regimes and changes in regulated stream systems in winter, and which factors may influence these changes
- Refinement of ice and temperature models

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 do 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
- Do peaking winter temperatures induce thermal stress in fish?
- Availability of drift and benthic feed in regulated stream 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 temp range 0-4, and with differently adapted populations
- Habitat preferences in winter and during ice formation – for modelling purposes

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