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Groundwater, critical habitats, and behaviour of Atlantic salmon, brown trout and Arctic char in streams

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Norwegian Institute for Nature Research

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Jan Heggenes
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Trondheim, December 2010

ISSN: 1504-3312

ISBN: 978-82-426-2235-8

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AVAILABILITY

Open

PUBLICATION TYPE

Digital document (pdf)

QUALITY CONTROLLED BY

Ola Ugedal

SIGNATURE OF RESPONSIBLE PERSON

Research director Kjetil Hindar (sign.)

CLIENTS

Directorate for Nature management (DN)

Norwegian Institute for Water Research (NIVA)

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KEY WORDS

- Groundwater
- Streams
- Substrate
- Hyporheic zone
- Juveniles
- Salmon
- Trout
- Char

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Abstract

Heggenes, J., Bremset, G. & Brabrand, Å. 2010. Groundwater, critical habitats, and behaviour of Atlantic salmon, brown trout and Arctic char in streams. – NINA Report 654, 28 pp.

Streams are characterized by turbulent hydraulic forces, varying discharge and temperatures, short water retention times, bedload transport and dynamic channel morphology. Alluvial groundwater is more stable with laminar flow, longer residence times, less variable temperatures, and constant sediment structure. Surface waters and groundwaters are closely connected in the hyporheic ecotone which can act as a source or sink, depending on complex physical and chemical spatial and temporal patch characteristics, direction and volume of flows, in-substrate pore space and connectivity, and movement patterns of organisms. Outflowing groundwater provides base flows, differs in temperature, dissolved oxygen levels and water quality from the surface water. Areas of groundwater inflow may at times provide moderated habitat conditions and possibly refugia for mobile stream salmonids.

A literature review suggests that groundwater may be important to salmonids by 1) modulating temperatures, 2) influencing water quality (nutrients, oxygen), 3) providing river base flows, and 4) providing refugia. It is well documented that salmonids may use groundwater inflow sites for behavioural thermoregulation to avoid near-lethal temperatures, and maintain energetically favourable body temperatures. Such thermoregulation may be effected through short vertical movements into the substrate, in particular for small fish, or through longer longitudinal movements. Such behaviour is observed during summer high temperatures and low flows, and at the onset of winter and ice formation. Actual field documentation varies among species, but it is likely a general behavioural strategy in mobile salmonids. Because of the local complexity in surface-subsurface and hyporheic flow connectivity and pattern in space and time, *in situ* studies are required. Spawning site selection, egg burial, overwinter egg survival and hatching time may be affected by groundwater inflow. However, the spatial and temporal complexity of groundwater flow integrated over time is a research challenge. It is well documented that groundwater flow may be critical in lacustrine spawning habitats. A general conclusion cannot be reached for lotic spawning habitats, probably because it varies locally.

The importance of groundwater in providing baseflows in summer and winter is rather obvious. Evidence with respect to the hyporheic refuge hypothesis is scarce and equivocal. Increasing evidence corroborates the function of the hyporheic zone, and associated groundwater flows, as a refugium for macroinvertebrates during low flow events in summer. However, little is known as to how young salmonids may use the hyporheic habitat in summer. In winter, the hyporheic zone is largely a daytime refuge for stream salmonids. Surprisingly, there is a lack of studies to substantiate the hypothesis that fish and macroinvertebrates may take refuge in the hyporheic zone in response to other environmental stressors, e.g. adverse chemical conditions.

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Sammendrag

Heggenes, J., Bremset, G. & Brabrand, Å. 2010. Groundwater, critical habitats, and behaviour of Atlantic salmon, brown trout and Arctic char in streams. – NINA Rapport 654, 28 sider.

Rennende vann er karakterisert av turbulens, fluktuerende vannføring og temperatur, kort oppholdstid, sedimenttransport og dynamisk elvemorfologi. Alluvialt grunnvann er mer stabilt med laminære strømningsforhold, har lengre oppholdstid, mindre temperaturvariasjon og konstant sedimentstruktur. Utstrømmende grunnvann gir en utjevning i tilsiget (basisvannføring), og skiller seg fra overflatevannet i temperatur, oksygeninnhold og vannkvalitet. Områder med grunnvannstilstrømming kan i perioder føre til endret habitat og kan utgjøre refugier for elvelevende laksefisk og andre mobile organismer.

En litteraturgjennomgang gir indikasjoner på at grunnvann kan være viktig for laksefisk gjennom 1) utjevning av temperaturforhold, 2) påvirkning av vannkvalitet (næringssalter, oksygen), mer stabil vannføring og 4) tilgang på refugier. Det er godt dokumentert at laksefisk gjennom atferdsbasert temperaturregulering benytter områder med grunnvann for å unngå subletale vanntemperaturer, slik at fiskene opprettholder kroppstemperaturer som er energetisk gunstige. Slik temperaturregulering kan oppnås gjennom kortere, vertikale forflytninger i bunnsubstratet, eller gjennom lengre forflytninger mellom vassdragsavsnitt. Det er observert slike atferdsmønstre i perioder om sommeren med høye temperaturer og lav vannføring, og likedan i perioder med isdannelse tidlig på vinteren. Det empiriske grunnlaget fra naturlige forhold varierer hos de ulike artene, men aktive forflytninger er trolig en generell strategi hos elvelevende laksefisk.

Overgangssonen mellom overflatevann og grunnvann viser stor variasjon i tid og rom, der vannføring, tilsig og geologi i bunn, bredd og nedbørfelt har stor betydning. Det er derfor nødvendig å gjennomføre feltbaserte studier. Viktige bestandsparametere som valg av gyteområde, graving av gytegroper, eggoverlevelse og klekketidspunkt kan påvirkes av grunnvannstilførsel. På grunn av temporal og spatial kompleksitet i grunnvannsforekomster er det en forskningsmessig utfordring å gjennomføre gode felteksperimenter. Det er godt dokumentert at grunnvannstilførsel er avgjørende for gyting i innsjøhabitat. På grunn av store lokale variasjoner er det ikke mulig å trekke en generell konklusjon for gytehabitat i rennende vann.

Det er åpenbart at grunnvann er viktig for å gi stabil vanntilstrømming gjennom året. Det er flere studier som viser at den hyporeiske sonen fungerer som et refugium for bunndyr i lavvannsperioder om sommeren. Imidlertid er det dårligere kjent i hvilken grad juvenil laksefisk benytter dette habitatet om sommeren. Om vinteren er den hyporeiske sonen i hovedsak et dagrefugium for juvenil laksefisk. Overraskende nok er det mangel på studier på hvordan fisk og bunndyr kan benytte hyporeisk sone som refugium ved ulike typer miljøstress, som eksempelvis ved alvorlige endringer i vannkvalitet (forsuring, kjemikalieutslipp mv.).

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Foreword

This project has been financed by research fundings from Directorate for Nature Management (DN), administrated by Atle Hindar at Norwegian Institute for Water Research (NIVA). The literature review has been conducted by Jan Heggnes in collaboration with Åge Brabrand and Gunnbjørn Bremset

The project is a part of a long-term research program focusing on the consequences of groundwater influx on eradication measures in rivers infected by *Gyrodactylus salaris*. Other parts of this program have focused on hydrological aspects, movements and abundance of juvenile salmonids in groundwater-fed areas of rivers and streams.

Trondheim, December 2010

Gunnbjørn Bremset, project manager

1 Introduction

Spatial and temporal distribution of source and sink habitats influence population regulation (e.g. Pulliam 1988). Particularly important habitats for an organism may have limited distribution in space and/or time, and therefore be deemed critical habitats. An understanding of the availability and use of such critical habitats is a prerequisite for conservation and wise management of species. The limited availability in space and time of such critical habitats and their use, however, also imply that they may be difficult to identify and characterize. In the recreationally and economically important freshwater salmonids, habitat and related individual fish behaviours may influence population regulation for example in salmon and trout (e.g. Milner et al. 2003). Because of their wide distribution and varied life histories in streams in northern temperate climates, they may experience extreme temporal (e.g. spates and summer droughts; Elliott 1994, winter temperatures and ice; Huusko et al. 2007) and spatial (e.g. stream order, substrates and micro-currents; Heggenes et al. 1999, Armstrong et al. 2003) habitat variation.

Rivers are characterized by turbulent hydraulic forces, varying discharge and temperatures, short water retention times, changing chemical conditions, bedload transport and dynamic channel morphology (e.g. Brunke & Gonser 1997, Power et al. 1999, Sear et al. 1999). In contrast, alluvial groundwater systems are more stable with laminar flow, long residence times, and largely constant sediment structure. Hydrologically, however, surface waters and groundwaters are closely connected in the hyporheic ecotone (e.g. Malard et al. 2002, Boulton 2007). This river-groundwater interface can act as a source or sink, depending on physical and chemical patch characteristics. Important factors are the direction and volume of flows and the usable in-substrate pore space and connectivity, in addition to patch stability (life span) and movement patterns of organisms. Outflowing (exfiltrating) groundwater can provide base flows, differ in temperature, dissolved oxygen levels and water quality from the surface water, be enriched in nutrients and prevent siltation (Brunke & Gonser 1997, Power et al. 1999). Consequently, areas of groundwater inflow may at times provide moderated habitat conditions and even refugia for stream salmonids that can easily respond to intermittent habitat conditions by behavioural movements (Økland et al. 2004, Heggenes et al. 2007). Interestingly, it has also been suggested that the hyporheic zone may act as shelter for benthos against anthropogenically induced toxic pulses (Jeffrey et al. 1986).

In this review we emphasize how juvenile trout, salmon and char may respond to spatio-temporal heterogeneous habitat conditions by behavioural movements, and the functional importance of the river-groundwater ecotone for these fish species. More specifically, the work was induced by the repeatedly negative results of attempted chemical treatment to eradicate the ectoparasite *Gyrodactylus salaris* from some west coast and northern rivers in Norway (Koestler & Brabrand 2001, Brabrand et al. 2005). Could infected juvenile salmon and Arctic char survive treatment periods in groundwater refugia, giving rise to re-infection of the salmon population?

2 Habitat mosaics and functions in the hyporheic ecotone

Traditionally, groundwater and rivers have been treated as distinct entities (e.g. Brunke & Gonser 1997, Boulton et al. 1998). However, a number of review papers over the last decade have pointed out the vertical connection and functional role and significance of the hyporheic zone (e.g. Brunke & Gonser 1997, Boulton et al. 1998, Malard et al. 2002, Boulton 2007). This vertical dimension remains understudied compared to longitudinal and lateral connectivity, perhaps for logistic and conceptual reasons. The streambed has been and is in many studies conveniently seen as a layer of uniform thickness and low saturated hydraulic conductivity (Leek et al. 2009), but it is not. The relative influx of surface water and groundwater is controlled by dynamic processes operating over a variety of spatial and temporal scales (Boulton et al. 1998, Alexander & Caissie 2003, Greig et al. 2007).

Additionally, hyporheic zone gradients can be characterized by hydrological, chemical, zoological and metabolic criteria, making construction of static concepts to represent ecological processes, difficult (Brunke & Gonser 1997). This may explain why there appear to be sufficient review and conceptual papers to justify much research (e.g. Orghidan 1959, Hynes 1983, Brunke & Gonser 1997, Boulton 2007), but surprisingly few empirical studies to substantiate a number of assumptions and speculations about the groundwater-river ecotone (Malard et al. 2002). Luckily this seems to be changing now (see below).

Recent empirical studies indicate the complexity and spatial patchiness of the hyporheic ecotone (Malard et al. 2002). New, improved sampling methods on relevant, i.e. generally small spatial scales (cm) have contributed importantly (Leek et al. 2009, Malcolm et al. 2009). Many, perhaps most rivers and streams are characterized by both vertical and longitudinal spatial heterogeneity within the streambed. For example, Leek et al. (2009) documented a high level of spatial heterogeneity (three orders of magnitude) in hydraulic conductivity (K) (**Figure 1**). They conclude such heterogeneity directly affects surface- and groundwater exchange and can have ecological implications for biogeochemical transformations, nutrient cycling, organic matter decomposition, and reproduction of gravel spawning fish. Indeed, both spatial (cm) and temporal (hours, days) fine scale variability of hyporheic hydrochemistry, in particular dissolved oxygen, appear to be common (**Figure 2**), and may affect e.g. egg survival in gravel spawning salmonids (Greig et al. 2007, Soulsby et al. 2009, Malcolm et al. 2009,). This variation is dynamic, depending on the relative contributions of fluxes of surface water and groundwater through the hyporheic zone, producing a fine scale spatio-temporal habitat mosaic. Brunke & Gonser (1997) conclude that “...*ecological studies...of the river-groundwater interface reveal an extraordinary patchiness and variability owing to the inherent heterogeneity of the physical parameters.*”

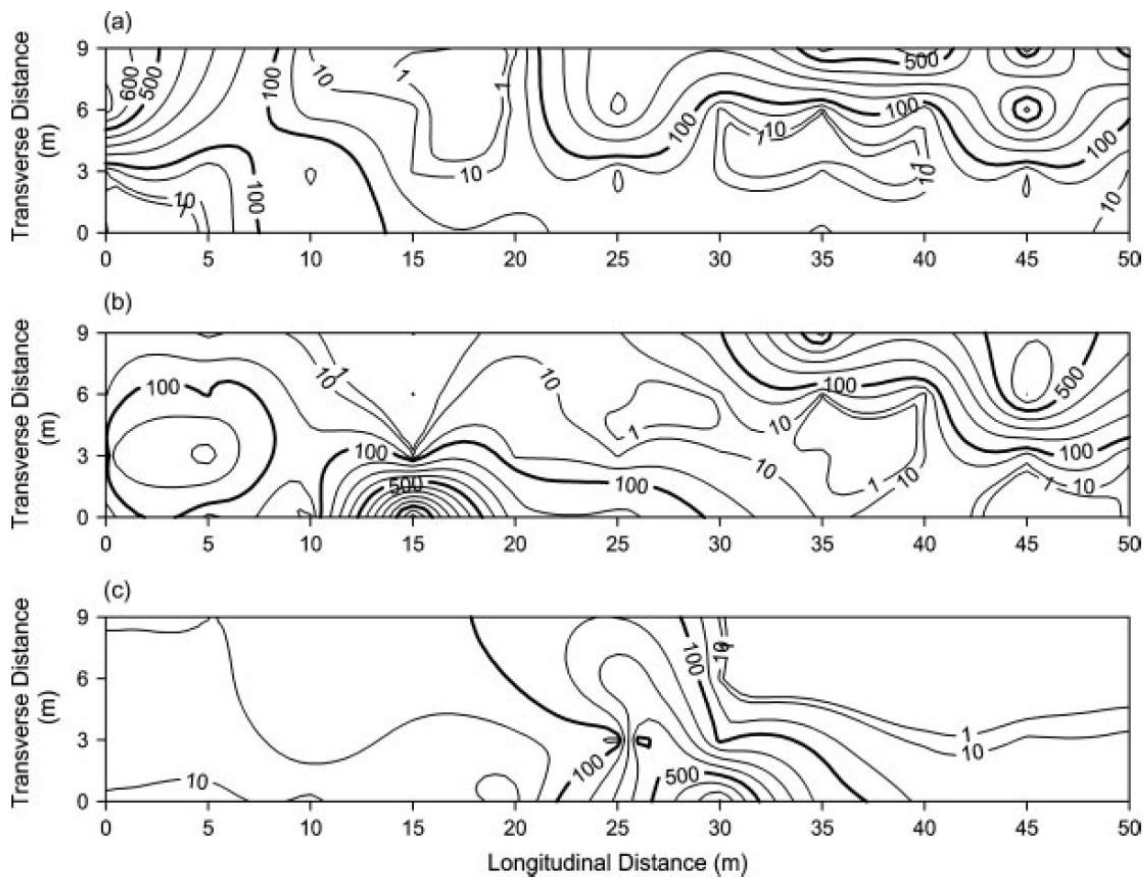


Figure 1. Saturated hydraulic conductivity ($m d^{-1}$) at a 50 m stream site for the depth interval (a) 0.30-0.45 m, (b) 0.6-0.75 m, and (c) 0.9-1.05 m (Leek et al. 2009).

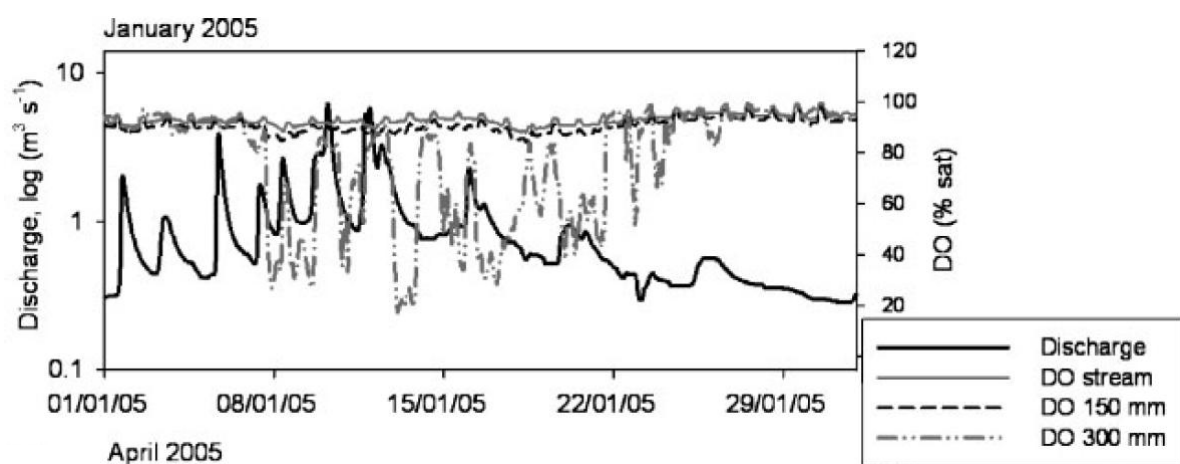


Figure 2. Dissolved oxygen dynamics in a small stream and hyporheic zone in January 2005. Note the spatial and temporal scales (Soulsby et al. 2009).

The hyporheic interstices are functionally a part of both the stream and groundwater ecosystems. The functional importance of the hyporheic zone for fish (and hyporheic assemblages) is largely controlled by the interstitial spaces (substratum composition: particle size, heterogeneity), flow rates and direction, sediment stability, and hydrological exchange processes determining temperatures, dissolved oxygen, and nutrients (e.g. Brunke & Gonser 1997, Boulton 2007). Boulton (2007) even suggest that these factors may form the basis for a habitat classification scheme (with associated conservation and management advantages), but does not work this out.

Thus the hyporheic zone may provide its inhabitants (e.g. Hansen 1975, Brunke & Gonser 1997, Malcolm et al. 2003):

- low velocity micro-niches (energy, shear stress),
- protection against extreme temperatures (winter ice formation, physiologically dangerous summer temperatures),
- protection against dessication,
- protection from large predators, and
- provide stable substrates during bedload movement

3 Groundwater in west-coast Norwegian streams

Westcoast, northern glacial areas are characterized topographically by deep confined valleys and steep sides, and geologically by (side- and end-) moraines, i.e. unsorted sediments, and old valley floors filled with glacial and alluvial deposits (**Figure 3**). With respect to influx of groundwater, geological mapping along the river shore should focus on three factors. First, topography will provide the potential for an aquifer and hydrostatic pressure differences. Second, geological heterogeneity will produce a potential for local underwater spring sites of groundwater flux. Third, characteristics of the hyporheic substrates in terms of sediment grain size and rock fracturing will determine microspatial influx sites.

The layering of tight and permeable layers in fluvial deposits, allow groundwater to follow permeable layers and to enter lakes and rivers as underwater seepage and springs. The runoff from the valley sides fills the pore spaces in these glacial-alluvial valley deposits with groundwater, resulting in a generally high water table. The groundwater gradually drains toward the valley bottom, feeding streams where the water table comes to the surface (**Figures 3 and 4**). These conditions are common in steep, glacially formed valleys and in areas with high annual precipitation, such as on the west coast of Norway, Iceland and Scotland, and in contrast to homogenous deep sand areas with low height gradient. Compared to the surface water, the rates of flow in groundwater aquifers are generally slow, governed by the hydraulic pressure head relating to the slope of the valley sides and the permeability (**Figure 3**; Power et al. 1999).

Groundwater inflow to inland Norwegian rivers may constitute 40-100 % of total water discharge during low flow periods in late summer and winter, while in West coastal rivers the total groundwater inflow is usually lower, or show higher variation, due to steeper topography (Colleuille et al. 2005). For example, the underwater influx into Lake Røldalsvatn, a typical Norwegian west coast lake, is micro-spatially largely dependent on the substratum. In areas dominated by gravels, the influx rates were measured to 1000-4000 ml m⁻² min⁻¹. Following rainfall 20-23.08.2004 the relative importance of surface water increased (**Figure 4**, Brabrand et al. 2002), thus pressing the groundwater-surface water interface down into the river bottom, confirmed by temperature measurements at site 2 and 3 following surface water temperature regime from 20.08.2004. Measurements of influx rates into rivers below river surface will follow the same pattern, and probably be of the same order of magnitude. Recharge is provided by the generally high rainfall and annual snowmelt, but is low in winter due to water being stored in snow and ice.

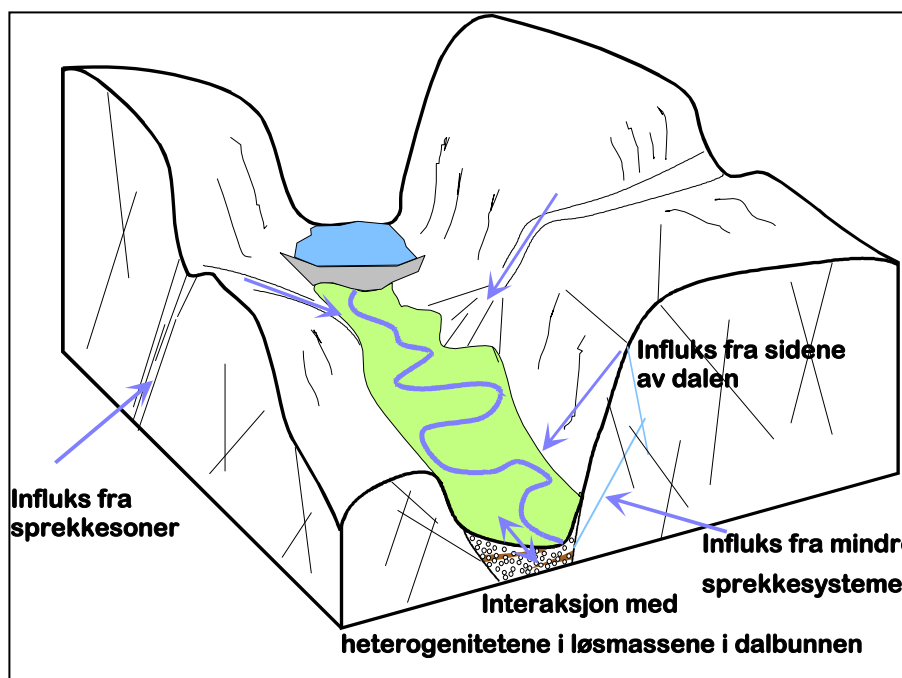


Figure 3. In areas where dense layers (fine sand, clays) alternate with permeable layers (gravel), concentrated groundwater inflows to streams are expected (Koestler & Brabrand 2001).

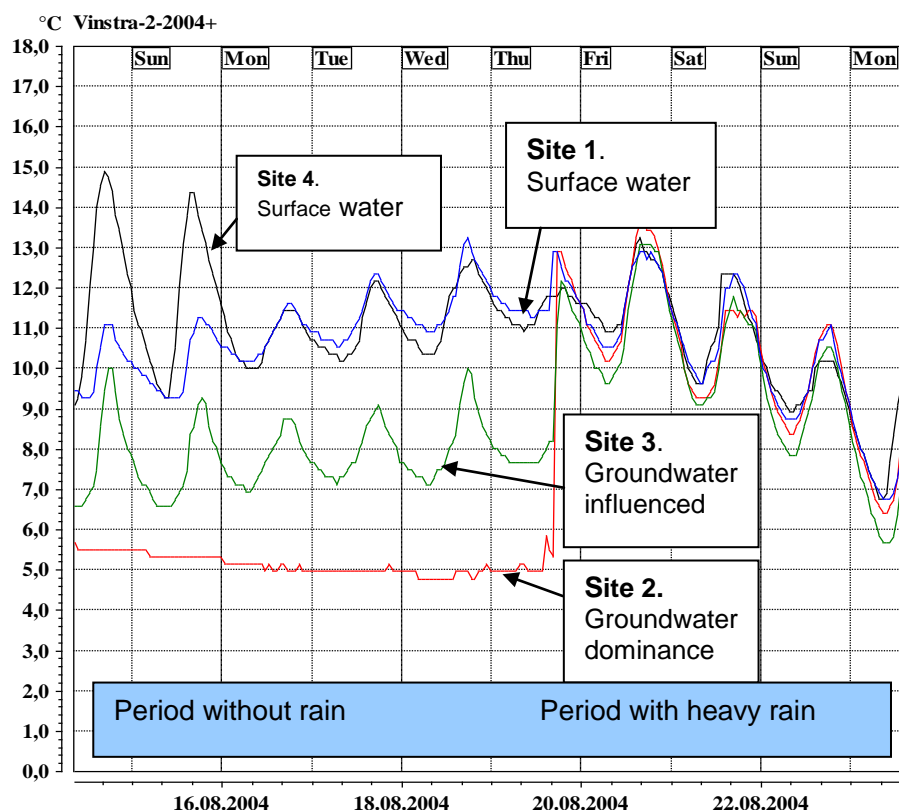


Figure 4. Water temperatures at four sites on river bottom in an area influenced by groundwater in the Vinstra river, showing that level of interface between groundwater and surface river water depends on river discharge (Brabrand et al. 2002).

4 Ice phenomena

Northern rivers, constituting a major part of the distributional range of stream salmonids, have a hydrology dominated by glaci-fluvial geology and climatic seasonality (see e.g. Prowse and Ommanney 1990, Power et al. 1999), of which winter ice phenomena is particularly relevant in this context. Ice means that a proportion of the mean annual discharge is locked up, but more importantly that flow patterns and temperatures of the rivers are influenced during considerable parts of the year (e.g. Power et al. 1999), and physical conditions and habitat suitability are directly changed by ice phenomena (e.g. Huusko et al. 2007, Linnansaari et al. 2009, Stickler et al. 2010). Whereas surface ice can create conditions that allow juvenile salmon to use habitats with limited in-stream cover, the formation of solid anchor ice might preclude access for juvenile salmon (Linnansaari et al. 2009). In addition to effects on physical habitat, ice formations can affect erosion processes and water chemistry.

River ice comes as surface or shelf ice, frazil ice, and anchor ice. Surface ice grows out from the river banks. It has been speculated that it may provide overhead cover for fish (Power et al. 1999), but there is little empirical evidence to substantiate this (Heggenes et al. 1993, Linnansaari et al. 2009, Stickler et al. 2010). Frazil ice, i.e. disc or needle-shaped ice crystals in super-cooled water, may have an important indirect effect on the hyporheic zone by adhering to the stream bed and building up anchor ice. Thick ice coatings on the bottom may trap fish in hyporheos in the substratum for prolonged periods (Stickler et al. 2010) and reduce hydrological exchange as to reduce dissolved oxygen levels, and may build up to modify and occlude the stream channel. It may form ice dams and back up water, or float away and release parts of the substratum. Frazil ice may also have direct deleterious effects on fish through plugging and damaging gill tissue (Brown et al. 1994). In particular small streams in cold, alpine environments, may freeze, at times even solid, in winter, so as to cause juvenile fish mortality and ensuing recruitment failure (Borgstrøm et al. 2005)

5 Microhabitat and behavioral movements in heterogeneous streams

The general in-stream habitat use by young salmon, trout and char strongly influence their distributions and abundances, and is rather well documented based on physical in-stream characteristics (**Figure 5**), e.g. water depth, velocity, substrate particle size, cover, but to a lesser extent to temperature and oxygen (Bremset & Heggenes 2001, Armstrong et al. 2003, Klemetsen et al. 2003). Uncertainties in predictive modeling of population regulation and effects of habitat availability and changes largely stem from the complexity of interactions between environmental variables, and between salmon, trout, char and their predators and competitors (Armstrong et al. 2003, Klemetsen et al. 2003, Milner et al. 2003).

One consistent result across salmonid species and studies, however, is that individuals select micro-niches providing low snout water velocities to reduce energy cost of holding position (Nislow et al. 1999, Hayes et al. 2000, 2007) In fastflowing streams this means that they generally hold position close to the bottom (**Figure 6**).

However, data on if and how salmon, trout and char may actively use the hyporheic zone (and therefore the functional significance) are largely lacking. The common method of direct (underwater) observation will not observe fish that are actually in the substrate, and electrofishing cannot separate fish that were in the substrate.

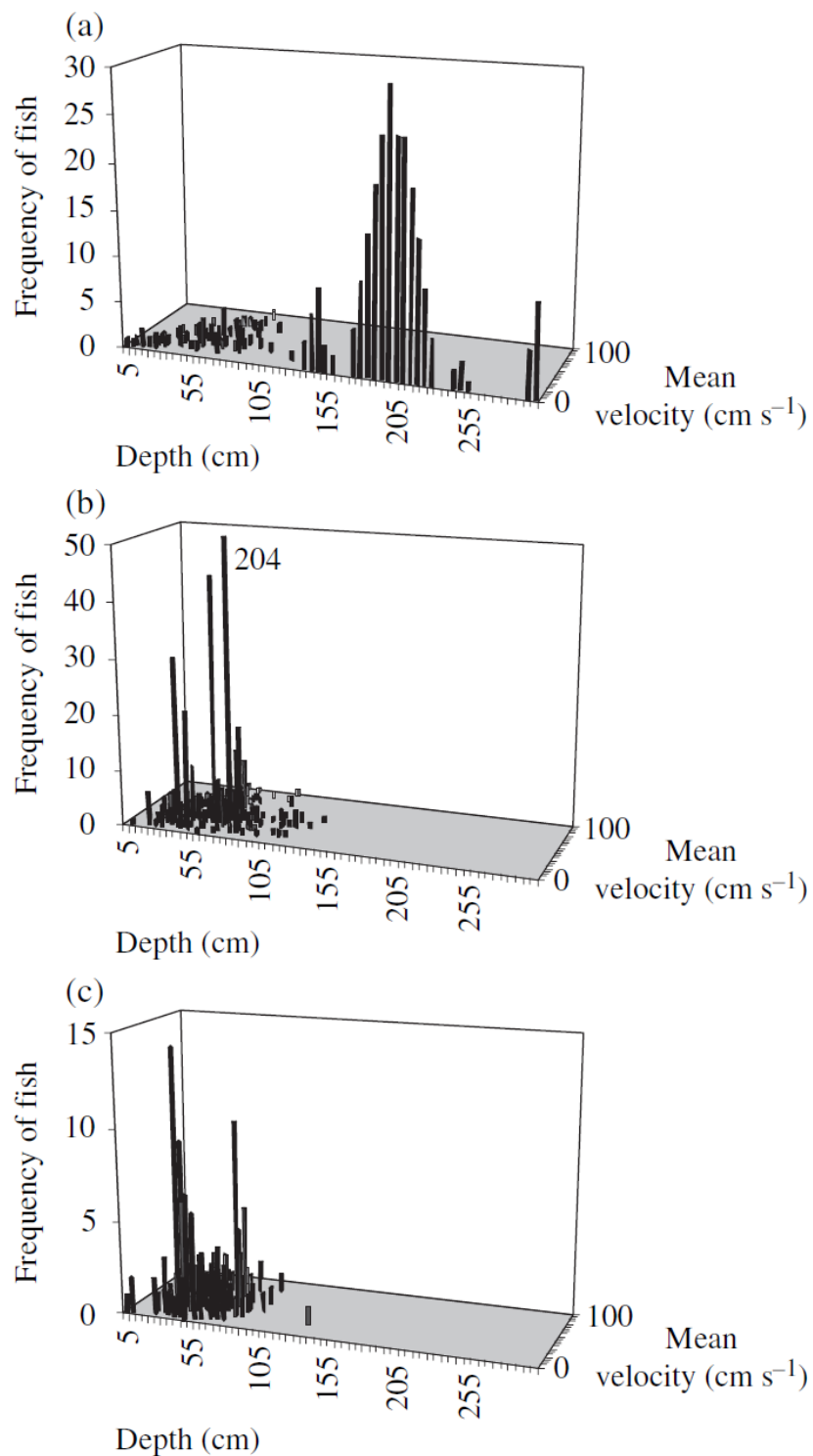


Figure 5. Summer habitat use for the variables water depth and mean water velocity for sympatric Arctic char (a), Atlantic salmon (b) and brown trout (c) in two Arctic rivers, Northern Norway (Heggenes & Saltveit 2007).

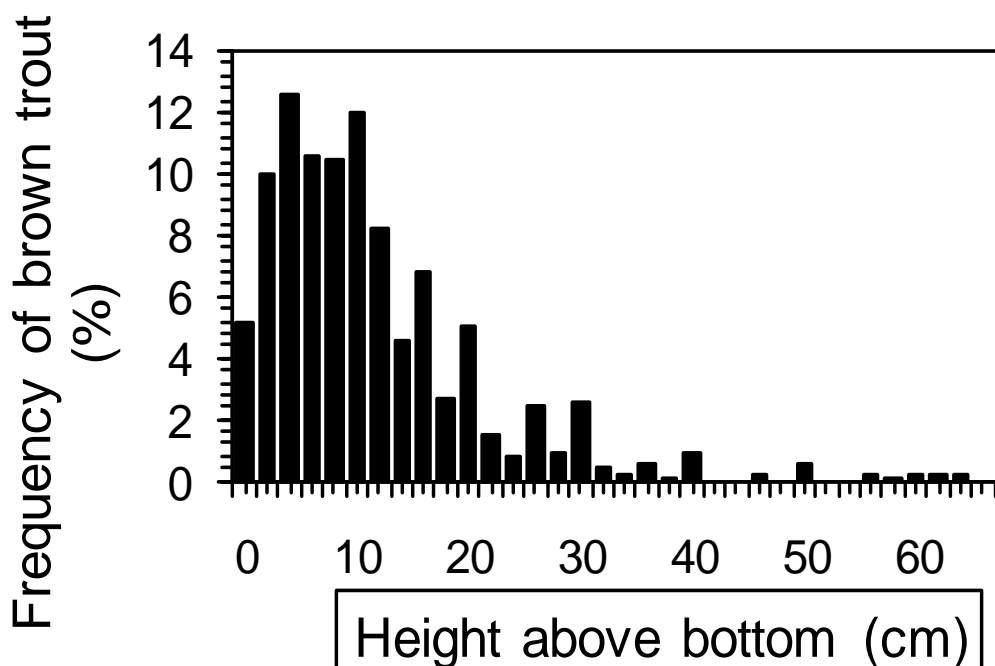


Figure 6. Height above bottom (cm) for holding positions of brown trout across eight rivers (Heggenes et al. 2002).

6 Behavioural thermoregulation

The temperature of groundwater is stable relative to surface water and also to annual mean air temperature. Groundwater upwelling habitat patches may therefore provide thermal refugia both in winter and summer (**Figures 2 and 4**), or energetically profitable thermal habitat patches. Such thermal habitat selection in summer is mostly related to high daytime temperatures in warm streams impairing growth and approaching severe stress and lethal levels for salmonid species. Temperature-dependent habitat selection has been demonstrated for e.g. young lake-dwelling brook and lake trout (*Salvelinus fontinalis* and *S. namaycush*; Biro 1998, Snucins & Gunn 1995, Curry et al. 1997), and cutthroat trout (*Oncorhynchus clarki*; Boxall et al. 2008) and adult Chinook salmon (*Oncorhynchus tshawytscha*) in streams (Berman & Quinn 1991, Torgersen et al. 1999). Baird & Krueger (2003) found that brook and rainbow trout (*Oncorhynchus mykiss*) throughout the summer maintained body temperatures significantly lower than ambient stream temperatures (difference 2.3 and 1.5°C, respectively, increasing to 4.0 and 2.5°C as river temperatures rose above 20°C), by moving to groundwater inflow pool habitat patches, and also cooler tributary confluences. Thus groundwater upwelling provided critical summer habitats for behavioural thermoregulation (see also Matthews & Berg 1997, Ebersole et al. 2001).

Environmental impacts such as water flow and temperature extremes appear to be particularly important for riverine salmonids (Breau et al. 2007, Riley et al. 2009). Although not yet documented, use of groundwater-influenced areas as temperature refugia may be expected during periods with super-cooled water and formation of frazil and anchor ice. Low flows and associated restriction of habitat, and temperature extremes, either in summer or winter, may cause mortality and population bottlenecks (Elliott 1994, Borgstrøm et al. 2005, Breau et al. 2007). In the Miramichi River, southeastern Canada, it has been documented extensive movements of salmon parr from mainstem areas to cooler tributaries during hot summer episodes (Breau et al. 2007). Juvenile salmon were also observed congregating in certain river areas with direct influx of groundwater in the streambed, or along river edges with groundwater seepage (Rick Cunjak, personal communication).

Similarly, Gibson (1966) observed brook trout and Atlantic salmon aggregating in a 17°C spring outflow in a river with ambient temperature 22°C. Young fish, e.g. young-of-year and 1+, may be small enough to find thermal microhabitats by short, vertical movements into substratum providing groundwater upwelling. Douglas (2006) reports that juvenile Chinook salmon may burrow in substrate providing groundwater upwellings, and to extensive depths, as a thermoregulatory behaviour, i. e. maintain temperatures at 16-17°C compared to ambient river temperatures of 23-25 °C, i.e. close to lethal levels for many salmonids.

Longitudinal or sideways movements and/or better local survival by larger fish in summer in suitable temperature habitats, was inferred by Boxall et al. (2008) for cutthroat trout living in high-altitude desert streams. On a landscape level, trout numbers were highest in transition zones between less confined and more confined valley segments, and greater valley confinement. These topographic characteristics suggest high groundwater input, i.e. thermal refugia (**Figure 1**) both in summer and winter. For brown trout, Olsen & Young (2009) found little effect of small and shallow coldwater patches in a New Zealand river, but trout were observed within a cold-water plume at the mouth of a spring.

It is generally believed that winter is a critical period for riverine salmonids (Cunjak & Power 1987, Cunjak et al. 1998), and overwinter mortalities may be high and suitable winter stream habitat restricted by ice phenomena (e.g. Power et al. 1999). Although results with respect to the regulatory role of winter are conflicting (Huusko et al. 2007), groundwater inflow areas may clearly provide stable (temperatures, flow) and ice-free habitats for overwintering fish and eggs.

7 Hyporheic habitat in summer

Comparative summer studies using underwater observations or electrofishing suggest that young char may spend considerable time concealed in the substrate (Heggenes & Saltveit 2007, see also Holierhoek & Power 1995), as opposed to young salmon and trout that normally hold position above river bed (see Bremset 2000). There are, however, to our knowledge no studies that investigate how, when and to what extent salmonids actually use the hyporheic habitat in summer, with the exception of eggs and alevins emerging from the redd in spring (Greig et al. 2007, Malcolm et al. 2009, Soulsby et al. 2009). The importance of groundwater is inferred from indirect effects, e.g. groundwater providing base flows and temperature refugia (Power et al. 1999).

Power et al. (1999) observed that higher summer temperatures appear to impair growth of older brook trout, but not 0+ and one year old fish. From this they speculate that these juveniles "*may be small enough to find suitable thermal microhabitats in the substratum and avoid unsuitably high temperatures*". However, there are no drifting invertebrates available when holding position in the substratum, so presumably juvenile fish would come out at night to feed. This speculation has yet to be substantiated, but behavioural homeostatic movements to maintain a suitable thermal regime is well documented (below). Small fish may move vertically into the substrate to find thermal refugia, whereas larger fish may move longitudinally in the stream or sideways into small tributaries to seek out cooler water in summer. Such temperature refugia provided by groundwater flow may increase in importance towards the distributional limits of a species, i.e. more frequent temperature extremes (Barton et al. 1985, Bowlby & Roff 1986).

8 Hyporheic habitat in winter

To our knowledge there are no studies that focus on in-substrate activity by salmonids in summer (see above). There is, however, some empirical data from winter conditions. Direct underwater observations document a change in the behaviour of young salmon and trout at the onset of low temperatures in the fall and winter. They become nocturnal, actively using the substrate for sheltering during the day (e.g. Rimmer et al. 1984, Heggenes et al. 1993, Bremset 2000, Harwood et al. 2002, Johnson & Douglas 2009, Stickler et al. 2010). This has been confirmed by carefully sorting through the substrate, and more recently by PIT-tag methodology. Whether they take advantage of small amounts of groundwater when sheltering in the substrate, is not studied or known. It is, however, known that other salmonid species may take advantage of groundwater upwellings in winter and actively seek out such patches (e.g. *Oncorhynchus clarki*, Brown 1999; *Oncorhynchus mykiss*, Baird & Krueger 2003; *Thymallus arcticus*, West et al. 1992; *Salvelinus fontinalis*, Baird & Krueger 2003). For example, Brown (1999) observed that radio-tagged cutthroat trout, with decreasing temperatures at the onset of winter, moved (on average 1 km) from solitary positions to aggregations in ice free areas. Fish stayed in aggregations, moved little (within 120 meter stream length), and mean size of aggregations correlated negatively with stream temperature. Fish moved when their habitats were occluded by anchor ice, suggesting hyporheic groundwater flow sites functioned as winter refugia. Similar results were reported by Harper & Farag (2004).

9 The hyporheic refuge hypothesis

The potential for the hyporheic zone to act as a refugium for mobile stream organisms during hydrological and environmental perturbations has been acknowledged for more than fifty years. Yet the evidence to support this is scant and equivocal (Wood et al. 2010 and references therein). In a recent study of stream invertebrates, Wood et al. (2010) discuss this hyporheic refuge hypothesis for stream macroinvertebrates and with particular reference to low flow conditions. In a temperate stream field study, they document increased use of the hyporheic zone by macroinvertebrate benthos, in particular *Gammarus pulex*, during the latter stages of a summer drought, correlating both with increased temperatures and reduced flow. Notably, the abundance of obligate hypogean macroinvertebrates in the hyporheic zone, also increased. The study emphasizes the need to consider surface-subsurface and hyporheic connectivity when assessing responses to disturbance in streams.

It has been suggested that benthic macroinvertebrates, and indirectly the even more mobile salmonids, may move out of a stream area or take refuge in the hyporheic zone, in response to adverse chemical conditions (Jeffrey et al. 1986, Brunke & Gonser 1997). Although it sounds plausible, we are not aware of studies that actually show such adaptive responses. It is, however, well documented that free swimming salmon and trout may exhibit avoidance responses to adverse chemical conditions (e.g. Åtland & Barlaup 1995, 1996, Åtland 1998). If groundwater outflow provide more suitable chemical conditions, this may indirectly suggest use of the hyporheic zone as a refuge.

10 Fish mobility and response to low flow

Habitat use in spatially and temporally heterogeneous streams may depend critically on the mobility of individual fish. Salmon, trout, and char are mobile species exhibiting large individual and temporal variation in movement patterns and propensity to settle or reside in a home area or explore (e.g. Armstrong et al. 1997, Økland et al. 2004, Heggenes et al. 2007). They have the capacity to respond to environmental variation and impacts on virtually any natural temporal and spatial scale by behavioural movements to shift habitat, e.g. to groundwater flow patches to find suitable temperatures (above). It is therefore important to maintain connectivity in streams. In theory, movement may be expected to be a typical response to (local) adversity. Additionally, the ideal free distribution model (e.g. Fretwell & Lucas 1970) state that movement may be a response to adjust fitness in a spatially and temporally variable environment, i.e. salmon, trout and arctic char would move to optimal habitat patches.

In general, it does not appear to be the case that all individuals of salmon, trout and char exhibit such fixed optimal behavioural movement responses (e.g. Økland et al. 2004, Heggenes et al. 2007). First, there appear to be a significant element of randomness in movement patterns. Second, there is substantial individual variation in movement patterns and behaviours. Third, habitat preferences, site fidelity and territoriality/home ranges may interfere with (short-time) optimal movement responses. Fourth, individuals do not have perfect knowledge of local habitat-fitness variation neither in space nor in time. Therefore, we would expect behavioural movement responses to any (acute) environmental impact to be complex, variable and to some extent unpredictable. Indeed, in a small-scale experiment Armstrong et al. (1998) found response of salmon parr to acute reductions in water flow to be variable, and the majority of the experimental parr remained in shallow areas prone to dewatering. There appeared to be “*no strong selection for mechanisms facilitating emigration from shallow areas in which fish would soon die should drought intensify*” (Armstrong et al. 1998).

In an evolutionary perspective, this will of course depend on the predictability, e.g. seasonality, of the environmental impacts (e.g. Slobodkin & Rapoport 1974). Remaining in shallow areas may generally be a fitter option than moving to pools during routine droughts, but not during rare and unpredictable extreme droughts or anthropogenic and often rapid reductions in water flow. In accordance with this, in small streams that regularly dry up in summer, anadromous trout and salmon tend to emigrate at unusually early life stages (Borgstrøm & Heggenes 1988, Jonsson & Jonsson 2002). At the onset of winter, juvenile salmonids may move to suitable overwintering areas (Petersson 1982), e.g. congregate in groundwater upwelling habitat patches (see above).

Dewatering experiments simulating regulated peaking flow regime support this. More rapid dewatering and shorter habituation time increase stranding of trout and salmon (Saltveit et al. 2001, Halleraker et al. 2003). Interestingly, highest frequency of stranding occurred during the first experimental drawdown, and was low or negligible in the second to fifth repeats, probably reflecting individual variation in movement response patterns, i.e. environmental selection, and possibly also individual “learning” (Flodmark et al. 2002, 2006, Halleraker et al. 2003).

An explanation for remaining in the shallow areas that was not explored in these experiments was potential survival in the shallows during dewatering by moving into the substrate, in particular in groundwater upwelling habitat patches. Although not much studied in young Atlantic salmon, brown trout and char, it is documented that juvenile Chinook salmon (*Oncorhynchus tshawytscha*) may burrow in substrate providing groundwater upwellings and to extensive depths (above, Douglas 2006). Unfortunately, active use of the hyporheic zone by Atlantic salmon, brown trout and Arctic char is hitherto almost exclusively studied with respect to redd site selection, egg deposition and survival, and fry development to the swim-up stage.

11 Redd site selection and egg development

Reproductive habitats are a necessity for population sustainability, and scarcity or poor quality of suitable spawning habitat may affect salmonid populations directly. Selection of spawning sites is species specific. Arctic char spawn in lakes or slow rivers, and may select upwelling areas (Cunjak et al. 1986), although this is not generally documented. Other salmonid species may also select spawning sites where upwelling, increasing flow and oxygen supply, occurs and/or upwelling increase egg survival (*Salvelinus fontinalis*: Blanchfield & Ridgeway 1997, Ridgeway & Blanchfield 1998, *Salvelinus confluentus*: Baxter & McPhail 1999, Baxter and Hauer 2000, *Onchorhynchus* sp.: Garrett et al. 1998, Geist 2000, Geist et al. 2002). The use of favourable groundwater inflow sites for spawning and juvenile fish survival is well documented. Several char species select groundwater outflow sites for spawning and juvenile habitat (e.g. Curry & Noakes 1995, Curry et al. 1995).

Brown trout and Atlantic salmon deposit their eggs in streams in the substrate in constructions called redds. Published studies on redd site selection typically examine substrate particle sizes, water velocities and water depths, generally considered the most critical microhabitat variables for redd site selection, in addition to vorticity (Crowder & Diplas 2002). Recent meta-analyses of brown trout and Atlantic salmon redd habitat indicate optimal water depths, velocities and substrate size of 15-45 cm, 20-55 cm s^{-1} and 16-64 mm for trout, and somewhat deeper and faster habitats for salmon (20-50 cm, 35-80 cm s^{-1} , respectively, **Table 1**; Louhi et al. 2008, Finstad et al. 2011). There have been some attempts to develop suitability criteria indexes for salmonid spawning habitat in particular for substrate particle sizes (Louhi et al. 2008, Wollebæk et al. 2008).

Although wide ranges of spawning habitats are utilized, related to available habitat, river, and fish size (Champigneulle et al. 2003, Zimmer and Power 2006, Wollebæk et al. 2008), the "window" for suitable substrate particle sizes is less variable, in particular with respect to fines (Table 1, see details in Louhi et al. 2008, Finstad et al. 2011). For example, brown trout and Atlantic salmon require spawning areas with little fine sediments and high oxygen levels (**Table 1**, Acornley & Sear 1999). They may still use substrate sizes from c. 0.1 mm (Louhi et al. 2008) to about 10 % of their body length (Kondolf & Wolman 1993) for spawning, but reasonable egg survival and hatching success requires a much narrower particle size range (Soulsby et al. 2009) because sufficient oxygen supply is critical (**Figure 2**; Greig et al. 2007, Malcolm et al. 2009, Soulsby et al. 2009). The critical percentage of fines decreases as dominant fine particle size decreases, and critical percentage of fines may be as low as 1.5% for very fine clay and silt (<0.125 mm; Louhi et al. 2008). Early eggs are less sensitive than late eggs. There is a positive correlation between size of spawning salmonids and water depth, velocity and substrate size (Kondolf & Wolman 1993, Louhi et al. 2008, Johnson et al. 2010).

The importance of groundwater for redd site selection and egg survival appears obvious (Soulsby et al. 2005), yet there is not much research to substantiate the idea that groundwater outflow directly affect spawning site selection by trout and salmon. Perhaps this is because groundwater outflow may in some cases be relatively poor in oxygen and decrease egg survival (Soulsby et al. 2005), while in other cases provide oxygen combined with a benign thermal environment and thereby increase survival (Hannah et al. 2004, Greig et al. 2007). Therefore, varying patterns of groundwater-surface water interactions may generate complex fine-scaled spatial and temporal mosaics and consequently complex conditions for egg survival (Malcolm et al. 2009). Hansen (1975) found similar density of brown trout redds in areas with and without groundwater inflow and it is certainly not a requirement in streams (Acornley 1998). On the other hand, groundwater inflow providing flow and oxygen to spawning sites appears to be important in lacustrine environments (Brabrand et al. 2002, Heggenes et al. 2009).

Table 1. Stream habitats used by brown trout and Atlantic salmon for spawning.

Brown trout			
Depth mesohabitat	Range	15-45 cm	Louhi et al. 2008
	Range	6-82 cm	Shirvell & Dungey 1983
	Range	23-215 cm	Wollebæk et al. 2008
	Mean	25.5 cm	Witzel & MacCrimmon 1983
	Mean	31.7 cm	Shirvell & Dungey 1983
	Means	20-49 cm	Heggberget et al. 1988
	Means	27-52 cm	Zimmer & Power 2006
	Mean	103 cm	Wollebæk et al. 2008
Velocity mesohabitat	Range	20-55 cms ⁻¹	Louhi et al. 2008
	Range	11-80 cms ⁻¹	Witzel & MacCrimmon 1983
	Range	15-75 cms ⁻¹	Shirvell & Dungey 1983
	Range	2-124 cms ⁻¹	Wollebæk et al. 2008
	Mean	46.7 cms ⁻¹	Witzel & MacCrimmon 1983
	Mean	39.4 cms ⁻¹	Shirvell & Dungey 1983
	Means	27-55 cms ⁻¹	Heggberget et al. 1988
	Means	23-50 cms ⁻¹	Zimmer & Power 2006
Substrate particle size	Range	1.6-6.4 cm	Louhi et al. 2008
	Mean	0.69 cm	Witzel & MacCrimmon 1983
	Means	5-8 cm	Heggberget et al. 1988
	Mean	7 cm	Wollebæk et al. 2008
	Critical % fines < ca. 2 mm	> 10 %*	Crisp & Carling 1989
	Mean	15.2 cm	Louhi et al. 2008
			Crisp & Carling 1989
Depth in gravel of egg burial	Mean	12 cm	Heggberget et al. 1988
	Minimum	14 cm	Witzel & MacCrimmon 1983
Atlantic salmon			
Depth mesohabitat	Range	20-50 cm	Louhi et al. 2008
	Range	15-40 cm	Moir et al. 1998
	Mean	38 cm	Beland et al. 1982
	Means	40-51 cm	Heggberget et al. 1988
	Mean	24.8 cm	Moir et al. 1998
	Means	23-43 cm	Moit et al. 2002
Velocity mesohabitat	Range	35-65 cms ⁻¹	Louhi et al. 2008
	Range	35-80 cms ⁻¹	Moir et al. 1998
	Mean	53 cms ⁻¹	Beland et al. 1982
	Means	39-80 cms ⁻¹	Heggberget et al. 1988
	Mean	53.6 cms ⁻¹	Moir et al. 1998
	Means	54-74 cms ⁻¹	Moir et al. 2002
Substrate particle size	Range	1.6-6.4 cm	Louhi et al. 2008
	Range	2-6.4 cm	Moir et al. 2002
	Means	7,8-12,5 cm	Heggberget et al. 1988
	Median range	1.9-2.5 cm	Moir et al. 1998
	Median range	2.1-3.5 cm	Moir et al. 2002
	Median	2.1 cm	Moir et al. 1998
	Mean % fines < ca. 1 mm	5.4	Moir et al. 1998
	Mean % fines < ca. 1 mm	4.1-8.3	Moir et al. 2002
	Critical % fines < ca. 2 mm	>10 %*	Crisp & Carling 1989
			Louhi et al. 2008
Depth in gravel of egg burial	Mean	15.2 cm	Crisp & Carling 1989
	Mean	18 cm	Heggberget et al. 1988
	Means	15-25 cm	Finstad et al. 2011

* Decreases with decreasing fine particle size.

12 Conclusion: Groundwater provide critical habitat for fish

Power et al. (1999) stated that the importance of groundwater to fluvial fishes stem from: 1) modulation of temperatures, 2) influences on water quality (nutrients, oxygen), 3) provision of base flows, and 4) provision of refugia. It is well documented that salmonids may use groundwater inflow sites for behavioural thermoregulation to avoid near-lethal high or low stream temperatures, and also to maintain an energetically more favourable body temperature than that provided by ambient stream temperatures. This behavioural thermoregulation may be effected through short vertical movements and burrowing into the substrate, in particular for small, i.e. 0+ and one-year-old, fish, or through longer longitudinal or sideways (into tributaries) movements to seek out groundwater flow. Such movements may be particularly common during summer high temperatures and low flows, and at the onset of winter and ice formation. Although actual field documentation may be more limited for some salmonid species than others, it is likely that this is a general behavioural strategy in mobile salmonids. How extensive such behavioural thermoregulation through movements is *in situ*, requires *in situ* studies, because the surface-subsurface and hyporheic flow connectivity and pattern in space and time tend to be very dynamic and complex.

Spawning site selection, egg burial, overwinter egg survival and hatching is also affected by groundwater inflow. Although perhaps more studied than behavioural movements, for stream spawning salmonids focus has been more on water velocities, depths and substrate composition during spawning site selection, and substrate fines and oxygen supply during winter, than on potential effects of groundwater flow *per se*. Due to that egg is an immobile life stage of salmonids, the spatial and in particular temporal complexity of groundwater flow integrated over time make such studies difficult. We may conclude that groundwater flow may be critical in lacustrine spawning habitats, whereas a general conclusion is difficult to reach for lotic spawning habitats. Most likely there is no general conclusion, except that *in situ* studies on groundwater flow in spawning sites are required.

The importance of groundwater in providing baseflows during droughts in summer and mid to late winter is rather obvious. More disturbing is the equivocal and limited documentation on groundwater and the hyporheic zone providing refugia. Increasing evidence corroborates the rather unsurprising function of the hyporheic zone, and the associated subsurface groundwater flows, as a refugium for macroinvertebrates during low flow events in summer. However, little is known about how in particular small salmonids may use the hyporheic habitat in summer, both during normal or low flows. In winter, stream salmonids often use the hyporheic zone as a day-time refugium (due to predation risk?) and emerge (in order to feed?) at night. More surprising is the apparent lack of studies to substantiate the idea that fish and macroinvertebrates may take refuge in the hyporheic zone in response to other environmental stressors, e.g. adverse chemical conditions.

13 References

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NINA Report 654

ISSN: 1504-3312

ISBN: 978-82-426-2235-8



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