

Master's thesis

**Densities of Atlantic salmon (*Salmo salar* L.) fry in
relation to physical habitat, spawning redd distribution
and parr abundance in a small subarctic river**

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19.06.2014

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Nerg Sami P.M: Densities of Atlantic salmon (*Salmo salar* L.) fry in relation to physical habitat, spawning redd distribution and parr abundance in a small subarctic river

Master's thesis: 38 p.

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June 2014

Keywords: Atlantic salmon, habitat selection, intercohort competition, *Salmo salar*, spatial distribution

ABSTRACT

Two small-scale surveys were conducted in a small river to examine the effects of physical habitat characteristics, spatial spawning redd distribution and abundance of older juveniles on the Atlantic salmon (*Salmo salar* L.) fry (age 0+) distribution 1) shortly after the emergence and 2) after the assumed main dispersal period of fry. The effect of physical habitat variables (water depth, water velocity and substratum size), spatial spawning redd distribution and densities of older juveniles were examined using multiple linear regressions. Identical models were fitted with generalized habitat suitability indices to test their applicability to predict the variation in fry densities. Clear patterns of habitat use were found in relation to individual physical habitat variables and suitability indices, but there was a large variation in densities, with this variation often being largest within optimum habitats and the capability of regression models to explain this variation was relatively poor, ranging from 22 to 34 %. It is suggested that physical habitat variables may rather act as limiting edges than determinants of habitat selection of fry at within-reach scales. Fry densities were not significantly related to densities of older juveniles. Spatial spawning redd distribution was positively correlated with fry density approximately 2 months after the emergence. This result supports previous findings that the spatial distribution of spawning areas is an important factor that affects habitat selection of Atlantic salmon fry.

JYVÄSKYLÄN YLIOPISTO, Matemaattis-luonnontieteellinen tiedekunta

Bio- ja ympäristötieteiden laitos
Kalabiologia ja kalatalous

Nerg Sami, P.M. Akujoen 0+-ikäisten lohenpoikasten (*Salmo salar* L.) tiheydet:
Fysikaalisen habitaatin, kutupesien spatiaalisen jakautumisen ja
vanhempien poikasten tiheyden vaikutukset habitaatinvalintaan
pienessä subarktisessa joessa
Pro gradu: 38 s.
Työn ohjaajat: FM Panu Orell, Dos. Timo J. Marjomäki
Tarkastajat: FT Jukka Syrjänen, Dos. Timo J. Marjomäki
Kesäkuu 2014

Hakusanat: habitaatinvalinta, lohi, *Salmo salar*, spatiaalinen jakautuminen, vuosiluokkien välinen kilpailu

TIIVISTELMÄ

0+-ikäisten lohenpoikasten (*Salmo salar* L.) elinympäristön käyttöä ja -valintaa suhteessa fysikaalisiin habitaattimuuttujiin (virrannopeus, vesisyvyys ja vallitseva pohjan raekoko), kutualueiden spatiaaliseen sijaintiin sekä vanhempien lohenpoikasten tiheyksiin tutkittiin pienellä subarktisella Akujoella. Tutkimus toteutettiin kahtena eri ajankohtana: 1) pian poikasten soraikosta nousun jälkeen ja 2) oletetun levittäytymisvaiheen jälkeen. Habitaatinvalintaa tutkittiin monimuuttujaregressiomallien avulla kahta eri lähestymistapaa käyttäen: hyödyntäen paikalla tehtyihin habitaattimittauksiin pohjautuvaa ja yleistettyihin habitaatinsoveltuvuusindekseihin perustuvaa mallia. Havaittu habitaatinkäyttö vaihteli samoissa rajoissa ja kalat suosivat samanlaisia elinympäristöjä fysikaalisten habitaattimuuttujien suhteen kuin aiemmissa tutkimuksissakin on havaittu. Regressiomallien tulosten perusteella soraikosta nousseiden poikasten tiheysvaihtelua selitti pelkästään vallitseva pohjan raekoko (34 %) ja kesänvanhojen poikasten tiheyttä vesisyvyyden, virrannopeuden ja etäisyysmuuttujan (etäisyys kutupesistä) yhdistelmä (30 %). Soveltuvuusindeksimallit antoivat samankaltaiset tulokset molemmilla kerroilla, mutta mallien selitysaste oli heikompi. Vaihtelu poikastiheyksissä selittävien muuttujien suhteen oli suurta, mutta usein heterogeenistä ja suurinta mallien ennustamalla optimaalalueilla. Tulokset viittaavat siihen, että fysikaaliset ympäristömuuttujat tulisi huomioida mesohabitaattitasolla paremminkin sietoalueen rajoina kuin 0+-ikäisten lohien habitaatinkäyttöä ja -valintaa määräävinä tekijöinä ja muut mittaamattomat biottiset ja abioottiset tekijät määräävät toteutuneen habitaatinvalinnan tämän sietoalueen sisällä. Vanhempien lohenpoikasten tiheydellä ei havaittu olevan vaikutusta 0+-ikäryhmän habitaatinvalintaan näytealueilla. Huolimatta kutualueiden suhteellisen tasaisesta spatiaalisesta jakautumisesta tutkimusalueella, yli neljännes kesänvanhojen poikasten selitetystä tiheysvaihtelusta selittyi etäisyydellä kutupesistä. Tiheys kasvoi sitä mukaa, mitä lähempänä pesät sijaittivat. Tämä on sopusoinnussa aiempien kokeellisten ja luonnonpopulaatioissa tehtyjen tutkimusten kanssa ja viittaa siihen, että kutualueiden spatiaalinen jakautuminen voi olla merkittävä tekijä, joka säätelee lohen elinkierron varhaisvaiheiden populaatiodynamiikkaa.

Contents

1. INTRODUCTION	5
1.1. Habitat use and selection of juvenile Atlantic salmon	5
1.2. Habitat requirements, preference, use and selection	6
1.3. The role of spatial scale	7
1.4. Intracohort competition	9
1.5. Objectives of this study	10
2. MATERIALS AND METHODS	10
2.1. Study area	10
2.2. Spawning survey	11
2.3. Juvenile abundance survey	11
2.3. Habitat survey	13
2.3. Statistical analyses	13
3. RESULTS	15
3.1. Juvenile densities and spawning redd locations	15
3.2. Single-pass results vs. three-pass density estimates	16
3.3. Habitat survey	17
3.4. Habitat use and selection of fry	17
4. DISCUSSION	21
4.1. Habitat use and selection of fry in early July	21
4.2. Habitat use and selection of fry in late August	22
4.3. Effect of parr density	25
4.4. Habitat suitability index values vs. direct measurements	27
4.5. Sources of errors and uncertainty	27
4.6. Main findings of the study	29
4.7. Conclusions and recommendations	31
ACKNOWLEDGMENTS	32
REFERENCES	32

1. INTRODUCTION

1.1. Habitat use and selection of juvenile Atlantic salmon

During the last few decades, habitat use of Atlantic salmon (*Salmo salar* L.) in its juvenile freshwater phase has been extensively studied (see reviews by Gibson 1993, Heggenes *et al.* 1999, Bardonnet & Bagliniere 2000, Armstrong *et al.* 2003, Finstad *et al.* 2011). According to Finstad *et al.* (2011), the habitat use of juvenile Atlantic salmon is variable and diverse on both temporal and spatial scales, both within and among populations. Due to the complex life history of Atlantic salmon, this variation in observed habitat use is related to ontogenetic shifts (e.g. Erkinaro *et al.* 1997, Nislow *et al.* 1999, 2000), and this variation is also seasonal and diurnal (e.g. Heggenes *et al.* 1999, Heggenes & Dokk 2001, Mäki-Petäys *et al.* 2004). This variation in habitat use also reflects the variation and interaction between abiotic factors, which interact in complex webs with biotic factors (Heggenes *et al.* 1999, Armstrong *et al.* 2003).

Typically, habitat studies have focused on the importance of physical habitat characteristics of the environment, which are considered to be the most important factors determining abundance, distribution and performance of salmonid fishes in streams (e.g. Heggenes *et al.* 1999, Armstrong *et al.* 2003). Consequently, habitat models developed for juvenile salmonids often attempt to explain the spatial variation in fish abundance by physical characteristics of the environment and when models are used for predictive purposes, they are typically based on empirical correlations between fish abundance and physical habitat variables (e.g. Bovee 1986, Fausch *et al.* 1988). According to Rosenfeld (2003) and Finstad *et al.* (2011), at least three fundamental types of predictive models are commonly used: Macrohabitat or distributional models, which predict the presence or absence of species at large spatial scales, habitat capacity models, which predict population size or density when a species is present, e.g. HABSCORE (Milner *et al.* 1993), and microhabitat models, which predict habitat use at fine spatial scales and are often used to create habitat suitability curves, e.g. PHABSIM (Bovee 1986).

According to Railsback *et al.* (2003), habitat selection models are widely used for management purposes, often with an underlying assumption that habitat with high density indicates high quality habitat and low densities indicate low quality, and populations respond positively to the availability of highly selected habitat. Thus, it is implicitly but potentially wrongly assumed that the observed density and habitat quality are always positively correlated and the highly selected habitat is directly related to high individual fitness potential or carrying capacity (e.g. Van Horne 1983, Garshelis 2000 cited in Railsback *et al.* 2003, Girard *et al.* 2004). For example, at very low densities, many suitable habitats may remain unoccupied or alternatively at high densities, fish may be observed in habitats that are potentially metabolic sinks (Rosenfeld 2003).

Many studies have shown that the relationships between salmonid abundance and physical habitat are often weak, exhibiting a large amount of unexplained variation (e.g. Terrell *et al.* 1996, Railsback *et al.* 2003, Hedger *et al.* 2005). The relatively poor transferability of many habitat models when applied to different regions and rivers is a well-known phenomenon (e.g. Armstrong *et al.* 2003), although there is also mixed (Guay *et al.* 2000, 2003) or contrasting results (e.g. Mäki-Petäys *et al.* 2002) which have shown that at least habitat suitability criteria is often more or less transferable between rivers.

Firstly, it is important to take into account the variation in habitat availability between rivers, which may influence the observed habitat use and selection (e.g. Heggenes 1990). Secondly, it is important as well to consider the potential interaction between physical habitat factors: preference for one habitat variable may be dependent or strongly modified on the levels of other variables (e.g. Armstrong *et al.* 2003, Finstad *et al.* 2011). Although habitat use and selection of Atlantic salmon juveniles in relation to certain physical habitat variables, such as water velocity, depth and substratum size, has been extensively studied, less attention has been paid to the interaction between these variables or to their relative importance (but see, e.g. Heggenes & Saltveit 1990, Bremset & Berg 1999, Girard *et al.* 2004, Hedger *et al.* 2005).

However, physical habitat factors are not the only determinants or limiting factors affecting salmonid abundance in the rivers (e.g. Armstrong *et al.* 2003). Numerous studies have shown that juvenile salmon distribution and abundance may be strongly influenced by several others but often unmeasured abiotic and biotic factors including: individual variability in preferences or feeding strategies (Heggenes *et al.* 1999, Roy *et al.* 2013), habitat heterogeneity (e.g. Dolinsek *et al.* 2007), territorial behaviour (e.g. Keeley & Grant 1995, Grant *et al.* 1998), stream flow (e.g. Heggenes & Dokk 2001), inter- and intraspecific factors including predation (Dionne & Dodson 2002, Vehanen 2003) and competition (e.g. Kennedy & Strange 1986, Fausch 1998, Bult *et al.* 1999, Gibson *et al.* 2008), limited mobility (Steingrimsson & Grant 2003), food availability (Vehanen 2003), temperature (e.g. Bult *et al.* 1999, Heggenes & Dokk 2001). Additionally, factors such as possible genetic adaptation to local habitats (Heggenes *et al.* 1999, Armstrong *et al.* 2003), variation in population abundance (e.g. Railsback *et al.* 2003), discontinuous nature of the suitable habitats (Railsback *et al.* 2003) and “limited individual habitat knowledge” (Railsback *et al.* 2003) may affect the observed habitat use.

1.2. Habitat requirements, preference, use and selection

Thus, when studying distribution and abundance of juvenile salmonids in the wild, it is important to distinguish the concepts of habitat requirements, preference, utilisation and selection (Rosenfeld 2003). According to Rosenfeld (2003), these terms are commonly used but sometimes misused in habitat studies, especially the concepts of habitat preference and selection.

“Habitat requirements are abiotic features of the environment that are necessary for the persistence of individuals or populations” (Rosenfeld 2003). This definition is similar to the well-known Hutchinson’s (1957) fundamental niche (although it originally included “both physical and biological” factors), wherein different habitat axes are the set of environmental conditions forming “the n-dimensional hypervolume” within which an organism can survive and persist, and each of these axes represents a potentially limiting environmental variable (Hutchinson 1957, Rosenfeld 2003). If a species has a complex life history with different ontogenetic stages, it will consequently have complex habitat requirements and thus these stages can be defined by different habitat requirements and corresponding niches (Rosenfeld 2003).

Moreover, it is useful to distinguish subsets of abiotic factors within this fundamental niche, especially important is the spatial niche, i.e. physical characteristics of the environment (Heggenes *et al.* 1999). Numerous abiotic variables have been included in habitat studies of stream-dwelling salmonids, and their relative importance often depends on the scale at which they are studied (e.g. Heggenes *et al.* 1999). However, there seems to be consensus that the most important and thus most commonly measured physical habitat features affecting abundance, distribution and performance of stream dwelling salmonids

at meso- and microhabitat scales are water velocity, depth, substrate, and cover (Heggenes *et al.* 1999).

Habitat preference is an illustration of an organism's fundamental niche (Hutchinson 1957) and it is defined as habitat selection in the absence of biotic factors (Rosenfeld 2003). It is also assumed to be independent of availability of different habitats and consequently determined as a function of species innate requirements, i.e. physiology and behaviour (Rosenfeld 2003, Kaspersson 2010). Thus, in order to study the "true" preference, factors such as competition, predation risk and availability of different habitats must be controlled or isolated (Rosenfeld 2003).

Habitat utilisation is defined as use of habitat in a specific spatio-temporal context, i.e. at a particular site at a particular time (Heggenes 1999, Kaspersson 2010). It is an illustration of the realized niche (Hutchinson 1957), representing habitat use in the wild under prevailing biotic factors such as competition and predation (Rosenfeld 2003). Habitat utilisation cannot deviate from the total habitat availability and consequently it varies spatiotemporally both within and between rivers (Kaspersson 2010).

"Habitat selection in the wild represents habitat preference under the prevailing abiotic and biotic conditions in any particular stream" (Rosenfeld 2003) and it is the relation between habitat utilisation and habitat availability (Kaspersson 2010). Habitat selection, based on the principles of optimal foraging theory (reviewed by Wootton 1999), is generally seen as a result of trade-off between potential energy intake, swimming costs and risks (from predators and unfavourable environmental conditions) (e.g. Heggenes *et al.* 1999, Finstad *et al.* 2011). Variation in these factors causes individual variation in growth, survival and ultimately in reproduction success (Heggenes *et al.* 1999). Habitat selection can be demonstrated, for example, when fish occur at higher densities (positive selection) in particular habitat types (e.g. pools, riffles or glides, Rosenfeld 2003).

According to Rosenfeld (2003), data on habitat selection is often used to infer habitat preference and data on habitat selection obtained from in situ studies indeed form the basis for most quantitative habitat models, with the underlying assumption that this selection observed in the wild reflects requirement, i.e. fitness consequences of habitat use (Rosenfeld 2003). However, according to Rosenfeld (2003), the accuracy of this assumption has rarely been validated.

1.3. The role of spatial scale

One important factor in habitat–fish relationship studies is the role of spatial context, i.e. the scale and the resolution in which they are conducted (e.g. Fausch *et al.* 2002, Lapointe 2012, Torgersen *et al.* 2012). One implicit assumption in many habitat studies conducted within reach scales and consequently, as noted by Teichert *et al.* (2011) also in applied models (e.g. PHABSIM, Bovee 1986) appears to be that fish are able to freely choose their position in the stream, according to the physical habitat characteristics of the environment. Habitat models are often derived from subsamples of stream reaches and then expanded to unsampled areas to predict fish distribution and abundance (e.g. Fausch *et al.* 2002). However, due to the large spatial scale of many Atlantic salmon rivers (L'Abée-Lund *et al.* 2004, Ugedal & Finstad 2011) juveniles may not be able to use or select all suitable habitats, and despite the potential suitable conditions, distribution and abundance of Atlantic salmon juveniles are often nonuniform within rivers (Finstad *et al.* 2011) due to many reasons such as migration barriers, fishing mortality affecting substock abundance (e.g. Johansen *et al.* 2008), or distance from suitable habitats that are required at earlier life stages (Finstad *et al.* 2010), combined with limited dispersal abilities or

restricted movements of juveniles (e.g. Crisp 1995, Webb *et al.* 2001, Steingrímsson & Grant 2003, Einum *et al.* 2008). These factors may have a large influence when interpreting fish abundance–habitat relationships.

As emphasized by Kocik & Ferreri (1998), although the freshwater habitat use of Atlantic salmon has been extensively studied, most studies have typically focused on the importance of requirements for particular life history stages (i.e. spawning, fry, parr and seasonal shifts). In other words, many studies have not taken into account the spatial arrangements of different habitats required for different subsequent life stages and consequently may have ignored the relationships between these habitats that may be important in limiting their selection by fish. Consequently, not only the overall amount of suitable habitats for different life stages, but also their spatial arrangements within rivers is likely an important factor that affects population dynamics and thus overall freshwater production of Atlantic salmon (Kocik & Ferreri 1998, Finstad *et al.* 2010).

Especially the youngest juveniles, age 0+ fish (young of the year, YOY or fry, hereafter term fry is used to describe the stage from emergence to the end of first summer) are shown to have relative limited mobility, with the majority of offspring staying within few hundred meters from their natal sites during the first summer (e.g. Beall *et al.* 1994, Crisp 1995, Garcia de Leaniz *et al.* 2000, Webb *et al.* 2001, Foldvik *et al.* 2010, Teichert *et al.* 2011). This observed limited dispersal may be related to energetic costs (Einum & Nislow 2005, Einum *et al.* 2006) and vulnerability to predators (Garcia de Leaniz *et al.* 2000), potentially combined with the discontinuous nature of available habitat and “lack of individual habitat knowledge” (Railsback *et al.* 2003).

Atlantic salmon females dig nests, which as aggregates form redds and wherein they deposit from hundreds to thousands of eggs depending on the size and fecundity of fish (e.g. Fleming 1996, Taggart *et al.* 2001, Fleming & Einum 2011), thus creating localised patches of high fry density at the emergence. Amount of the available spawning habitat can be highly variable among rivers and often the distribution of suitable sites is nonuniform, or even sparse and clumped within rivers (Moir *et al.* 1998, 2004). Furthermore, annual salmon spawning runs are often variable (e.g. Jonsson *et al.* 1998) thus potentially causing variation in the actual yearly usage of suitable spawning sites. Additionally, females might select or compete for the same ideal spawning sites (e.g. Taggart *et al.* 2001).

As a result, eggs are often distributed nonuniformly in relation to suitable nursery habitat for fry (e.g. Foldvik *et al.* 2010). These factors combined with the previously mentioned limited dispersal abilities of fry (e.g. Beall *et al.* 1994, Crisp 1995, Garcia de Leaniz *et al.* 2000, Webb *et al.* 2001, Foldvik *et al.* 2010) and density dependent mechanisms such as high mortality rates during the early posthatch stage (e.g. Einum & Nislow 2005) and reduced growth during the later stages (Grant & Imre 2005, Imre *et al.* 2005) can create a large spatial variation in population dynamics of Atlantic salmon at relatively small spatial scales as shown in experimental and manipulative studies during the recent years (Nislow *et al.* 2004, Einum & Nislow 2005, Einum *et al.* 2006, 2008).

However, the effect of spatial spawning redd distribution on subsequent juvenile density distribution is relatively little studied in natural populations of Atlantic salmon (but see Foldvik *et al.* 2010 and Teichert *et al.* 2011) and the relationship between spatial redd distribution and the subsequent spatial variation in density of fry in the wild during the early phase shortly after emergence remain unknown.

1.4. Intracohort competition

According to Einum & Nislow (2011) and Nislow *et al.* (2011), competition between juvenile Atlantic salmon of the same age-group is a well-described mechanism affecting population dynamics, and the effects of density dependent population regulation of fry during the first weeks after emergence are also known (Nislow *et al.* 2004, Einum & Nislow 2005, Einum *et al.* 2006, 2008). Density-dependent intracohort habitat selection is also a well-known phenomenon (reviewed by Einum & Nislow 2011, Nislow *et al.* 2011), although there has been contrasting results whether this selection is following patterns of ideal free (Fretwell & Lucas 1970) or ideal despotic (Fretwell 1972) distribution (e.g. Bult *et al.* 1999, Girard *et al.* 2004, Hedger *et al.* 2005, Gibson *et al.* 2008).

However, competition between different cohorts of juvenile Atlantic salmon is generally less understood (Nislow *et al.* 2011). Atlantic salmon may stay in streams as juveniles even up to 7 or 8 years before migrating to sea especially in the area of its northernmost distributional range (Niemelä *et al.* 2000). Thus, juveniles originating from several different cohorts typically live in sympatry (e.g. Hutchings & Jones 1998) and consequently may potentially compete for same resources. It has been shown in both experimental studies and in the wild that survival, movements and growth of salmonid cohorts are affected by the density of older cohorts (e.g. Nordwall *et al.* 2001, Imre *et al.* 2005, Kaspersson & Höjesjö 2009, Kaspersson *et al.* 2012), and even vice versa (Einum & Kvingedal 2011, Einum *et al.* 2011). Results from experimental and manipulative studies also suggest that intercohort competition may affect the habitat selection of juvenile salmonids (e.g. Vehanen *et al.* 1999, Kaspersson *et al.* 2012).

Many studies have shown that habitat use of Atlantic salmon juveniles is often more or less size- and age-structured with larger individuals having considerably wider spatial niche than small juveniles, especially during the summertime (e.g. Heggenes *et al.* 1999). Smaller and younger juveniles, especially fry, typically utilize shallow habitats with fine substratum particle sizes and low velocities, whereas older and larger individuals tend to use to a greater extent deeper areas having higher velocities and coarser substratum sizes (Heggenes *et al.* 1999, Armstrong *et al.* 2003, Mäki-Petäys *et al.* 2004, Linnansaari *et al.* 2010). This observed pattern with intercohort segregation between fry and parr (hereafter age >0+ juveniles are called parr) is often related to avoidance of overlapping in resource use (e.g. Mäki-Petäys *et al.* 2004) or size-dependent differences of predation risk (e.g. Bremset & Berg 1999), but it may also reflect partly pure ontogenetic (i.e. size- and age-related) requirements and preferences for different habitats and resources (e.g. Nislow *et al.* 1999, 2000).

Considering the size-related territorial (e.g. Grant *et al.* 1998) and hierarchical behaviour (reviewed by Nislow *et al.* 2011) often associated to Atlantic salmon juveniles, where larger individuals or individuals having “prior residence advantage” (O’Connor *et al.* 2000, Harwood *et al.* 2003) are dominant over smaller or later arriving fish, it is also possible that this pattern may also be a result of intercohort exclusion from preferred habitats (Kaspersson 2010, Kaspersson *et al.* 2012), especially if the effects of spatial or temporal variation in abundance are taken into account.

As several cohorts of juvenile Atlantic salmon typically live within the same relatively confined areas in the wild, it is obvious that patterns of habitat utilisation of different age-groups overlap in a lesser or greater extent within stream habitat at mesohabitat scales (e.g. Kaspersson 2010). Thus, it would be expected that changes in parr abundance would potentially affect the habitat selection of fry. However, there is little evidence of negative effects of parr (age >0+) density on habitat use and selection of 0+

salmonids in the wild (but see Ayllón *et al.* 2013) and the potential effect of parr density on habitat selection of Atlantic salmon fry appears to be seldom included in habitat studies (but see Teichert *et al.* 2011).

1.5. Objectives of this study

The major aim of this thesis was to examine how much of the variation in density of a single cohort of Atlantic salmon fry (0+) is related to a combination of physical habitat variables and spatial spawning redd distribution at a single distinct nursery area in a small river i) shortly after the emergence of fry and ii) after the assumed main dispersal period of fry. For this purpose, measured physical habitat and distance variables were studied together, in order to also investigate their relative strengths and interactions. To investigate the potential effect of older juvenile abundance on habitat selection of fry, parr density was also included in models as an explanatory variable.

Secondly, the capability of generalized habitat suitability curves developed for Atlantic salmon fry (Heggenes 1990, Mäki-Petäys *et al.* 2002) to predict variation in fry abundance was also tested and these variables were also studied together, instead of treating them independently.

2. MATERIALS AND METHODS

2.1. Study area

The River Akujoki is a small tributary (length 35 km, drainage area 193 km²) of the large sub-arctic River Teno in the northernmost Finland (Fig. 1). The river supports a self-sustaining Atlantic salmon population with annual estimated spawning run varying from approx. 50 to 250 fish and the salmon population in the river is dominated by one sea-winter fish (1SW, grilse), which on average constitutes approx. 83 % of the yearly spawning stock (Panu Orell, Finnish Game and Fisheries Research Institute, FGFRI, unpublished data). Only lowermost 6 km of the river is accessible for anadromous salmonids due to a large waterfall. The only other species constantly present in this section is brown trout (*Salmo trutta* L.): with few occasional sea-run fish and the proportion of juveniles in the yearly electrofishing assessment has been low, typically less than 1–2 % of the total catch (FGFRI, unpublished data).

A large amount of the yearly spawning activity in the river has been observed to occur constantly in the uppermost 2.7 km long section below the waterfall (Fig. 1). The next observed spawning redds below this section have usually been found several hundred meters downstream, in the middle of a long rapid, thus creating a gap in the spatial spawning site distribution. This pattern in spawning distribution was also detected in autumn 2006. Therefore, this upper river section was chosen for the study site to represent a distinct single reproduction unit. The section is mostly shallow and fast flowing, dominated by rapids, glides and riffles and only three deeper pools exist in the section. Wetted width ranges from 5 to 35 m, max depth is < 1.5 m in rapids, glides and riffles and < 2.5 m in pools.

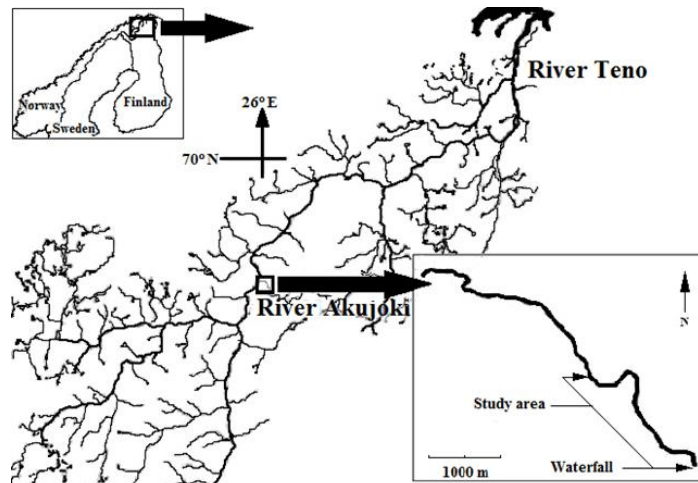


Figure 1. Location of the River Akujoki and the study area.

2.2. Spawning survey

Locations of spawning redds were observed by snorkelling shortly after the observed main spawning season had ceased at the end of September 2006. An experienced two-diver snorkelling team followed the procedure developed for assessing spawning stock of adult salmon (Orell & Erkinaro 2007). If necessary, replicate counts were made. Owing to the small size of the river, the clarity of water (lateral visibility in pools approx. 10 m) and the simple instream structure of the river, almost the whole riverbed was clearly visible during the survey. Observations were recorded with a GPS device (Garmin GPS 12) by an assistant, who followed the divers on the riverbanks.

As it is known that a female salmon may dig more than one redd (e.g. Taggart *et al.* 2001) and as in some areas there were partly overlapping redds or superimposition of redds making it hard to distinguish an individual redd, either a single redd or a cluster of redds was marked as a single source for egg deposition. Female salmonids also tend to dig test or “false” redds that are abandoned before egg deposition (e.g. Crisp & Carling 1989). These were distinguished by visual inspection: Observed excavated redds being small and short in their appearance and without a pot-tail -structure (Crisp & Carling 1989) were considered as false redds and these were abandoned from the final counts. No redds were opened to investigate the presence of eggs by removing the gravel as any mechanical disturbance may cause egg mortality during this stage prior to the eye pigmentation of eggs (e.g. Taggart 2001).

No sea-run or large-sized brown trout, i.e. trout similar to 1SW salmon in size were observed in the river during the snorkelling counts of salmon stock prior to spawning season in autumn 2006 (Panu Orell, FGFRI, unpublished data), and therefore all the observed redds were considered to be salmon redds.

2.3. Juvenile abundance survey

Densities of juvenile salmon were surveyed by semi-quantitative single-pass electrofishing (Hans Grassl GmbH ELT 60II/GI, non-pulsed DC at ~450 V, 0.2 A) with a standardized field procedure. The first electrofishing took place on July 5–10 2007, 4 days later after checking (by electrofishing as well) at 5 known redd sites located throughout the

study area that the fry were emerged. Second electrofishing survey took place on August 28–31 2007.

A non-pulsed direct current (DC) was used to reduce any possible harmful effects of electrofishing on fish (e.g. Snyder 2003), especially on larger juveniles and adult salmon present in the area. Due to the smaller immobilization zone of DC compared to pulsed DC and due to the size-dependent catchability of electrofishing (Bohlin *et al.* 1989), a special attention was paid to the field procedure: relatively short anode strokes and dense combing (< 1 m sideways steps were taken between each anode stroke) of area were used. The same standardized field procedure with the same personnel was used throughout the study: one person using anode, other person using dip net to capture fish and third person assisting the team in the riverbank.

Although single-pass method does not provide an estimate of the actual number of fish present in a certain area (Bohlin *et al.* 1989), it provides data on relative variation in abundance among sampling sites. The multi-pass removal method has a poor relative precision in areas containing few fish due to the wide confidence limits of density estimates (Bohlin *et al.* 1989, Julkunen *et al.* 1995). Due to the study design, this low abundance was expected to occur in several sampling units (i.e. transects). Although single-pass data typically contains noise due to variation in catchability, it was assumed that the spatial variation in abundance among transects would exceed the variation in site-specific catchability (Bateman *et al.* 2005). Furthermore, it has been shown in many previous studies that single pass-results correlate highly with multi-pass removal estimates (e.g. Kruse & Rahel 1998, Bateman *et al.* 2005).

Although it was not possible to compare directly single-pass results obtained from this study to three-pass estimates, data for estimating the relative precision of single-pass method was obtained from the electrofishing assessment of the River Akujoki from 5 different sites located below the waterfall from years 1989–2008 (FGFRI, unpublished data). In these data ($n = 14$), three-pass estimates were counted by a modified Moran–Zippin procedure (Bohlin *et al.* 1989, Julkunen *et al.* 1995), or if the yield was less than 15 fish, due to the limitations of Moran–Zippin method, a total catch per 100 m² was used as an index of abundance. The relative sampling error of three-pass estimates was measured as the coefficient of variation:

$$C = SE(\hat{y})/\hat{y},$$

where SE is the standard error of the estimate \hat{y} and \hat{y} is the estimate itself (Bohlin *et al.* 1989).

A total of 54 approximately 1.7 m wide transects across the river were electrofished starting from 50 and ending to 2700 m downstream below the waterfall. All transects were equally located at 50 m longitudinal intervals (measured with a tape measure from midpoint to midpoint, marked on the riverbank and spatially referenced with a GPS device) throughout the entire study area, except in two cases, where in both the two subsequent transects in pools were located in 60 (12. and 40.) and 40 (13. and 41.) meter intervals from previous ones due to too deep water for electrofishing. Mean area of electrofished transects was 38 m², ranging from 11 to 62 m². The single-pass catch from each transect was used as a relative index of abundance, divided by the area fished (wetted width (m) x 1.7 m) and counted as relative density index, fish/100 m² separately for 0+ and ≥1+ age groups of salmon.

The total length of all caught salmon fry and parr was measured to the nearest mm. As in the River Tenojoki watershed there is usually a clear gap between the lengths of 0+ and 1+ salmon age groups, i.e. length distributions of these age groups do not overlap, all

the fish < 45 and < 55 mm (1st and 2nd survey, respectively) in length were classified as fry (0+). In any uncertain case, a scale sample between the adipose fin and the lateral line was taken and aged by scale reading with a microfiche reader (60 x magnification) later ($n = 2$).

During the field work, subsamples from the fry catch (approx. 30–100 % of the fish caught, depending on the catch size) of each transect were collected for another study, which included microsatellite DNA analysis of fry. Results from the microsatellite DNA analysis showed that two trout fry were wrongly identified as salmon (Juha-Pekka Vähä, unpublished data) at two transects during the first electrofishing survey, and based on these results, fry densities were corrected for these transects.

2.3. Habitat survey

Physical habitat variables including water depth, water velocity and the dominant substrate size were measured and recorded from 5 equally divided points across each transect with starting and ending points located at 1 m from the shoreline, immediately after electrofishing. Depth was measured to a precision of 1 cm using a graduated pole. Mean water velocity was measured with a flow meter (Schiltknecht MiniAir 2 fitted with a 20-mm propeller) at 0.6 x water depth. Dominant substrate size was visually estimated on approximately $1/3$ m² area at each point using a wading shoe (32 cm in length) as a radius around the depth measurement pole. Substrate size was visually determined and classified using a modified Wentworth scale (in Mäki-Petäys *et al.* 2002, modified from Heggenes 1991), 0 = organic, 1 = 0.07–2 mm, 2 = 2.1–8 mm, 3 = 8.1–16 mm, 4 = 16.1–32 mm, 5 = 32.1–64 mm, 6 = 64.1–128 mm, 7 = 128.1–256 mm, 8 = 256.1–512 mm, 9 = 512.1–1024 mm, 10 = bedrock). As in the modified Wentworth scale each substrate particle size class increases from its predecessor by the constant ratio of 1:2, values of dominant substrate size data were recoded into continuous parameter for further analyses by replacing the classified values of each class with their corresponding numerical midpoint values.

In order to reduce observational errors, same person measured all variables throughout the study. During the second survey in late August, observed water depths differed very little (~1–2 cm) from those measured in early July. Therefore, all measurements from the first survey were used as such for the second survey as well.

To obtain habitat suitability index data, the measured habitat variable values were converted to a range of 0.0–1.0 (unsuitable–optimal) using the generalized habitat suitability index curves for salmon fry (0+, < 7 cm in length) developed by Heggenes (1990) and modified by Mäki-Petäys *et al.* (2002). Suitability index values were classified as follows (*sensu* Mäki-Petäys *et al.* 2002): > 0.75 = optimal, 0.50–0.75 = suboptimal, < 0.50 = unsuitable or poor for fry.

2.3. Statistical analyses

Data from the spawning redd survey and from electrofishing transects recorded with a GPS device were transferred to ArcGIS (ESRI, Redlands, USA). Distances between spawning redd areas and transects were calculated by linear measurements and treating the river as a one-dimensional line.

As habitat variables are interrelated with each other in streams and fish more likely respond to combination of these variables, rather than to single variables independently (e.g. Heggenes 1999, Guay *et al.* 2000, Armstrong *et al.* 2003, Girard *et al.* 2004), a multiple regression procedure was chosen to produce a description of the habitat use and selection of fry.

Multiple regression models with backward procedure (removal criteria = 0.10) were fitted between independent (physical habitat variables, distances from redds, parr density indices) and dependent variables (fry density indices) for both survey periods, early July and late August. Two outliers ($> 5 \times \text{SD}$ from the mean), fry density indices at transects 22 and 30 (50.6 and 121.4 fish /100 m², respectively, Figure 2) in early July, were removed from the analyses. For physical habitat variables, calculated mean values from each transect were used in the analyses. Based on the visual examination of variables and residuals, quadratic terms of all three physical variables were included in the models.

A single redd or a distinct cluster of redd area was treated as a single source for egg deposition in the analyses and it was assumed that the movements and dispersion of fry occurred only downstream. Results from several studies have shown that the movements and dispersal of fry typically occur primarily downstream (e.g. Beall *et al.* 1994, Garcia de Leaniz *et al.* 2000, Webb *et al.* 2001, Bujold *et al.* 2004, Einum *et al.* 2008, 2011, Foldvik *et al.* 2010, but see Einum & Nislow 2005).

The abundance or density of fry has been typically found to decrease rapidly within a range from several tens to few hundreds of meters downstream from the redds thus exhibiting leptokurtic patterns, and the detected maximum dispersion range has been observed to vary from few hundred meters up to 2.4 km, variation in the observed dispersal ranges depending on the time of observations after the emergence of fry and temporal differences in dispersal patterns (Gustafson-Greenwood & Moring 1990, Garcia de Leaniz *et al.* 2000, Webb *et al.* 2001, Bujold *et al.* 2004, Einum & Nislow 2005, Einum *et al.* 2008, Foldvik *et al.* 2010, Einum *et al.* 2011).

The assumption of a mere downstream dispersal was also partly supported by the results from microsatellite DNA analysis of the River Akujoki salmon fry. In these data, all the fry belonging to the same full or half sibling families and that were sampled during the second survey were found from the same transects or from transects located downstream when compared to the samples collected during the first survey (Juha-Pekka Vähä, unpublished data). Due to the study design, it was obvious that almost any particular transect, excluding the uppermost ones, could have been seeded from several redd areas. Although the true limits and the amount of dispersed fry from each particular redd area were unknown, a following formula was used to create a distance variable for regression analyses, as it, based on the visual examination of the data, had the best fit to describe the overall effect of redd locations on fry density in the study area:

$$\sum \sqrt{(1/d_i)},$$

where d_i is the distance in meters (m, range from 5 to 2665 m) from each transect (1.–54.) to each redd area located upstream.

An identical multiple regression procedure was also used to test the capability of generalized habitat suitability index curves (Heggenes 1990, Mäki-Petäys *et al.* 2002) to explain the variation in fry density in early July and late August surveys. For this purpose, mean values of physical habitat variables from each transect were replaced with their corresponding suitability index values. Otherwise, both models and procedures were identical to those fitted with measured physical habitat variables, thus also including both distance from redds and parr density as independent variables and quadratic terms of physical habitat suitability index values were added in the models if needed.

Assumptions of linearity (quadratic terms were included if needed), normality, and independency (Durbin-Watson statistics 1.55–2.42) were met in all four analyses. There was heteroscedasticity in the data obtained from the first survey due to large number of zero observations, but these patterns were not significantly improved even after

transformations and transformations also led to the violation of assumption of normality. Therefore, these data were not transformed. Due to heteroscedasticity, fry densities from the August survey were square-root transformed to better fit the assumptions of linear regression models. No multicollinearity was detected between independent variables. Due to the structural multicollinearity caused by quadratic interaction terms, each physical habitat variable and their corresponding suitability index variables were centered at their mean before quadratic terms were added. No multicollinearity was detected in these models (all VIFs in full models <2.4 and in final models <1.6). All models were considered final when single explanatory variables were significant at $\alpha < 0.1$. This level was chosen due to the relative small sample size and as it is known that the use of a more traditional level (e.g. 0.05) may fail to identify those habitat variables that are known to be important for habitat selection of salmonids in the rivers (e.g. Bryant *et al.* 2004, Ayllón *et al.* 2013).

To examine the relative precision of single-pass electrofishing method, a linear regression was fitted between three-pass estimates/total catches (independent variable) and first-pass catches (dependent variable) to the electrofishing assessment data of the River Akujoki. Variables were transformed to a logarithmic scale: $\ln(\text{single-pass density})$ and $\ln(\text{three-pass density} + 1)$ to better fit the assumptions of normality and homogeneity of variances.

All regression analyses were conducted by the SPSS version 20.0 for Windows (SPSS Inc. Chicago USA).

3. RESULTS

3.1. Juvenile densities and spawning redd locations

A total of 114 salmon fry and 448 salmon parr were caught in early July with a mean density of 7.9 fish/100m² for fry and 27.7 fish/100m² for parr (Table 1). In late August, total catch for fry was 254 and for parr 469 fish, with a mean density of 14.6 fish/100m² for fry and 26.7 fish/100m² for parr (Table 1, Fig. 2). In early July, almost half (25 of 54) of transects were completely unoccupied by fry (Fig. 2). Abundance of juvenile trout was low: mean density (all age groups combined) was 0,3 fish/100 m² in both early July (n = 4) and late August (n = 5) and trout were present only at 4 and 5 transects in early July and late August, respectively.

A total of 21 single redds or distinct cluster of redd areas were observed, located from 35 to 2475 meters downstream from the upper limit of the area (Fig. 2). Median distance between subsequent redds or redd areas was 102.5 meters, ranging from 11 to 554 meters.

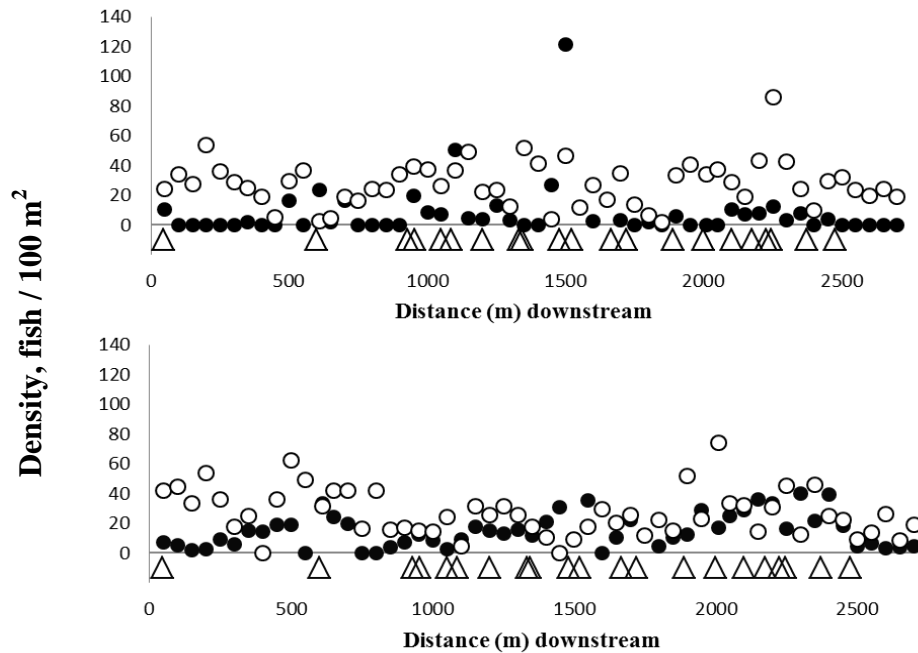


Figure 2. Density indices of salmon fry (solid dots) and parr (open dots) at transects ($n = 54$) in early July (upper panel) and late August (lower panel). Triangles indicate locations of observed redds or distinct redd clusters ($n = 21$).

Table 1. Density indices of salmon fry and parr (1= early July, 2 = late August, $n = 54$ for both) and values of physical habitat variables at transects ($n = 54$) for depth (d), water velocity (v), substrate (s , recoded to continuous parameter) and habitat suitability index values for fry (< 7 cm in length): $S(d)$, $S(v)$, $S(s)$ for depth, velocity and substrate size, respectively. Note: Habitat and habitat suitability index data pooled across each transect (number of measurements: 5 per each variable per each transect).

	Density (fish /100 m ²)				Habitat measurements			Suitability indices		
	fry1	fry2	parr1	parr2	d (cm)	v (m s ⁻¹)	s (mm)	$S(d)$	$S(v)$	$S(s)$
mean	7.9	14.6	27.7	26.7	28.8	0.45	239	0.91	0.81	0.65
SD	18.2	11.0	15.2	15.5	6.7	0.16	136	0.08	0.26	0.16
min	0.0	0.0	1.7	0.0	16.2	0.13	38	0.68	0.11	0.37
max	121.4	39.6	85.8	74.2	46.8	0.86	627	1.00	1.00	0.91

3.2. Single-pass results vs. three-pass density estimates

Examination of the data obtained from the electrofishing assessment of the River Akujoki showed that the first pass caught, on average, 58 % of the fry present, ranging from 42 to 78 %. In three-pass estimates, mean catchability for fry was 0.58 (SD = ± 0.13 , range 0.41–0.79, $n = 14$) and the average relative sampling error $C = SE(\hat{y})/\hat{y}$ was 11.6 %. There was a statistically significant and very strong correlation between log-transformed three-pass estimates and single-pass results: $R^2 = 0.984$, $R^2_{adj} = 0.982$, $p < 0.001$ (Fig. 3). Examination of the fitted model and data showed (back-transformed exponential values) that the average relative random error of single-pass results was approx. 16 % compared to three-pass results and single-pass electrofishing explained, on average, approx. 87 % of the variation in fry density estimated from three-pass electrofishing.

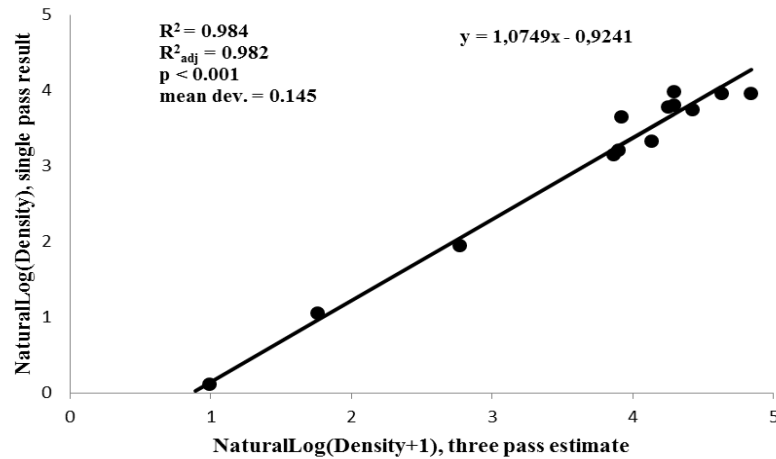


Figure 3. Fitted model and data showing relationship between log-transformed three-pass estimates and single-pass electrofishing results ($n = 14$). Data obtained from the electrofishing assessment of the River Akujoki from years 1989–2008.

3.3. Habitat survey

Measured and calculated mean (data pooled along each transect) values for water velocity varied from 0.13 to 0.86 m s^{-1} , for depth from 16.2 to 46.8 cm and for dominant substrate size from 38 to 627 mm (Table 1). Mean suitability index values for velocity varied from 0.11 to 1, for depth from 0.68 to 1 and for dominant substrate size from 0.37 to 0.91 (Table 1). Most of transects (91 %) provided optimal (> 0.75) mean depth suitability index values for fry (Table 2). Three quarters of transects were classified as optimal (> 0.75) for mean water velocity index value for fry and 85 % of transects provided at least suitable, sub-optimum (index value ≥ 0.5) dominant substrate size for fry (Table 2).

Table 2. Relative distribution (%) of mean habitat suitability index values of transects ($n = 54$). S(d), S(v), S(s) for depth, velocity and substrate size, respectively. Suitability value > 0.75 = optimal, from 0.50 to 0.75 = suitable, less than 0.50 = unsuitable or poor for fry. Note: Habitat index data pooled across each transect.

Suitability index class	S(d)	S(v)	S(s)
< 0.5	0	17	15
0.5–0.75	9	7	57
> 0.75	91	76	28

3.4. Habitat use and selection of fry

There was a statistically significant relationship between fry density and dominant substrate size in early July, and the final model explained 34.1 % of the variation in fry density (Table 3, Fig. 4). Predicted range of dominant substrate particle size for fry density was 38–346, 550–627 mm with a maximum predicted density occurring at 38 mm (Table 3, Fig. 4). Salmon parr density, distance from spawning redds, depth and velocity did not significantly affect the variation in fry density and were thus removed from the analysis during the backward selection procedure.

In late August, 30 % of the variation in fry density was explained by velocity, quadratic term for depth, and distance from spawning redds together (Table 3, Fig. 4). Ranges and predicted optimum (i.e. with predicted maximum density) values of physical habitat variables for fry density were: velocity 0.13–0.86 m s⁻¹ (optimum 0.13 m s⁻¹), depth 16–47 cm (optimum 29 cm). More than 25 % in the explained variation (semipartial squared correlation $sR^2 = 0.081$) and approximately 10 % of the total variation (if the effects of other explanatory variables were held constant, partial squared correlation $pR^2 = 0.104$) in fry density was related to the distance from spawning redds (Fig. 4). Increase in fry density was positively related to the shorter distance from spawning redds located upstream. Neither salmon parr density nor dominant substrate size significantly explained the variation in fry density and were consequently removed from the analysis.

Table 3. Final regression models explaining salmon fry density variation in the River Akujoki in early July (n = 52) and late August (n = 54). d = depth, v = water velocity, s = dominant substrate size, dist. = distance from spawning redds. S(d), S(v) and S(s) for depth, velocity and substrate size suitability index values, respectively. Note: * = dependent variable, fry density, square-root transformed. For partial and semipartial coefficients of determination for individual explanatory variables, see figure 4.

Early July					*Late August				
$R^2 = 0.341$ SEE = 5.643 p < 0.001					$R^2 = 0.30$ SEE = 1.424 p = 0.001				
Variable	B	SE (B)	β	p-value	Variable	B	SE (B)	β	p-value
constant	3.601	0.97		< 0.001	constant	2.926	0.470		< 0.001
s	-0.37	0.007	-0.731	< 0.001	v	-3.350	1.211	-0.336	0.008
s ²	0.00008	0.00003	0.369	0.015	d	-0.016	0.035	-0.064	0.653
					d ²	-0.009	0.003	-0.301	0.017
					dist.	2.250	0.942	0.333	0.021
Early July, fitted with suitability index values					*Late August, fitted with suitability index values				
$R^2 = 0.216$ SEE = 6.094 p = 0.001					$R^2 = 0.265$ SEE = 1.445 p = 0.001				
Variable	B	SE (B)	β	p-value	Variable	B	SE (B)	β	p-value
constant	4.898	0.845		0.027	constant	2.817	0.406		< 0.001
S(s)	20.781	5.604	0.464	0.001	S(v)	2.001	0.762	0.320	0.011
					S(d)	5.557	2.571	0.282	0.036
					dist.	1.591	0.881	0.235	0.077

Suitability preference index value for dominant substrate size explained 21.6 % of the fry density variation in early July (Table 3, Fig. 4). Salmon parr density, distance from spawning redds, habitat suitability index values for both depth and velocity did not significantly explain the variation in fry density and were therefore removed from the analysis.

Habitat suitability index values for velocity and depth combined with distance from spawning redds together explained 26.5 % of the fry density variation in late August (Table 3, Fig. 4). Salmon parr density and habitat suitability index value for dominant substrate size did not significantly explain the variation in fry density and were consequently removed from the analysis.

Overall, there was a large variation in fry density in relation to explanatory variables in all four cases (Fig. 4). In final models, variation in fry density typically increased as the

predicted optimality for a single explanatory variable or combination of variables increased, with this variation being mostly greatest in habitats having optimum or near optimum predicted values (Fig. 4). Similar patterns of unequal variation in densities were also present in some relationships between insignificant explanatory variables and fry abundance, for example in the relationship between fry density and velocity suitability index value in early July (Fig. 4). In early July, habitat use of fry had a considerably narrower range of spatial niche in relation to all physical habitat variables or to their corresponding suitability index values (two outlying data points were excluded from the data) and fry were less dispersed to transects than in late August (Figures 2 and 4, Table 4).

Table 4. Ranges (min-max among transect mean values) of physical habitat variables and habitat suitability index values used by fry in early July and late August. Habitat values for depth (d), water velocity (v), substrate (s, recoded to continuous parameter) and habitat suitability index values for fry: S(d), S(v), S(s) for depth, velocity and substrate size, respectively. Note: Habitat and habitat suitability index data pooled across each transect. Two outlying data points in early July removed from the data.

	Habitat measurements			Suitability indices		
	d (cm)	v ($\text{m}\cdot\text{s}^{-1}$)	s (mm)	S(d)	S(v)	S(s)
Early July	17.5–41.5	0.13–0.63	38–346	0.74–0.99	0.46–1.00	0.51–0.91
Late August	16.2–46.8	0.13–0.82	38–627	0.68–1.00	0.15–1.00	0.37–0.91

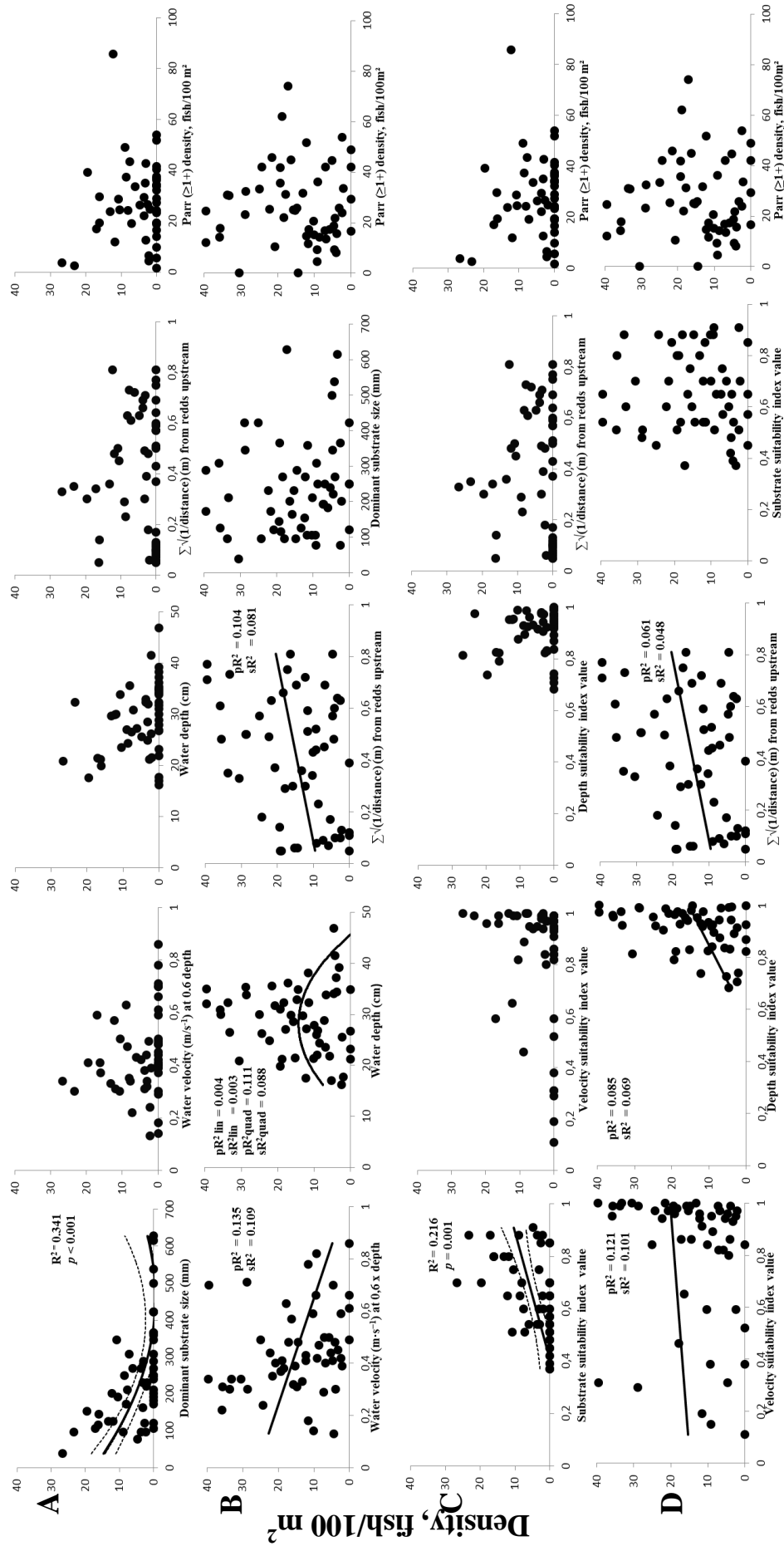


Figure 4. Relationships between fry density and independent variables A) in early July, B) in late August and C) early July and D) in late August with physical habitat variables replaced with their corresponding suitability index values. Final fitted models (Table 3) are shown with fitted regression lines; without regression line = non-significant variable, variable excluded from the final model. Note: Regression analyses for B and D were carried out on square-root transformed data for dependent variable, but regression lines shown in the graphs have been back transformed. In B and D fitted models are shown as partial models (other explanatory variables held constant); pR^2 's and sR^2 's indicate partial and semipartial coefficients of determination, respectively. Dashed lines indicate 95 % mean confidence intervals for regression lines. For full final model parameter estimates, see Table 3.

4. DISCUSSION

4.1. Habitat use and selection of fry in early July

In the present study, shortly after the emergence in early July, fry density was not significantly related to mean water velocity or depth. Nislow *et al.* (1999, 2000) found with an empirically validated foraging-based bioenergetics model that in early summer, approximately 1–2 months from onset of feeding, fry were consistently selecting microhabitats having low current velocities (0.08–0.18 m s⁻¹), despite their limited availability in the environment. Girard *et al.* (2004) found in their field study that bottom, snout and mean water velocity were highly intercorrelated for both the habitat used by fry and in the habitats available and the mean water velocity was the most important single variable, followed by depth, determining habitat selection of fry approximately 3–6 weeks after the emergence.

These statistically insignificant relationships found in the present study do not mean that depth and velocity were unimportant variables in determining habitat use of newly emerged fry at mesohabitat scales. The observed variation in density was unequal in relation to mean water velocity and fry were mostly found within a relatively narrow velocity range (0.13–0.63 m s⁻¹), thus suggesting that there was a positive relationship between these variables, although not revealed by the regression model. Furthermore, despite the variation in density, the observed habitat use of fry occurred almost exclusively within a relatively narrow range of mean depths (0.17–0.41 cm) during the first survey. That is, despite these insignificant relationships, ranges of mean water velocities and depths used by fry in this study were similar to those that for example Girard *et al.* (2004) found to be preferred by fry few weeks after the emergence: 0.06–0.48 m s⁻¹ for velocity and 20–39 cm for depth. However, in the present study timing of survey was different, representing even earlier stage, immediately after emergence.

Therefore, the ontogenetic requirements of newly emerged fry may have had a large role in habitat selection (Heggenes & Traaen 1988, Gustafson-Greenwood & Moring 1990, Garcia de Leaniz *et al.* 2000). Heggenes & Traaen (1988) found that the critical velocity values that small fry could tolerate were ranging from 0.10 to 0.25 m s⁻¹, with this variation depending on both temperature and the time from onset of swim-up during the first two weeks. Downstream displacement started at lower velocities, but fry also actively searched for low-velocity niches. They also observed that the typical position of newly emerged fry was only approximately 4–6 mm from the bottom in a smooth-bottomed experimental channel. However, in natural streams water velocity is substantially lower near the bottom than in the mean column (e.g. Allan & Castillo 2007), and especially coarse gravel and cobble provide velocity refuges (Gustafson-Greenwood & Moring 1990) for fry and potentially also protection against predators (Garcia de Leaniz *et al.* 2000). These above-mentioned factors may explain, why in the present study dominant substrate size alone explained more than one-third of the variation in fry density in early July, thus also suggesting that these areas with coarse gravel-cobble substrates are very important for newly emerged fry by providing suitable microhabitats (Gustafson-Greenwood & Moring 1990, Nislow *et al.* 1999, 2000, Garcia de Leaniz *et al.* 2000).

In addition to habitat selection, these patterns may also imply that fry were still mostly occupying areas in the immediate vicinity of their natal sites. This pattern of limited and relatively slow early dispersal has been typical in previous observational studies (e.g. Gustafson-Greenwood & Moring 1990, Garcia de Leaniz *et al.* 2000). Spawning habitats may occur in areas having relatively high water velocities and substrate particle sizes are

typically smaller in spawning habitats than in those reported to been used or selected by fry (reviewed by Armstrong *et al.* 2003).

Perhaps surprisingly, in the present study, variation in fry density was not related to the distance from spawning redds in the first survey in early July. The overall observed low abundance (mean density 7.9 fish per 100m²) at transects and that almost half of the transects (25 of 54) were completely unoccupied by fry, suggest that the fry dispersion was still very limited and the spatial resolution of the study, representing mesohabitats across the river with 50 meter intervals, combined with early timing, was too coarse, thus unable to detect any spatial associations between spawning redds and fry abundance. This coarse resolution most likely also prevented the detection of deeper associations between fry density and other physical variables, which should have to been studied at finer scales. It is also possible that the timing of the first survey was too early, although all the fry sampled during the preliminary checkout and the first survey had no external yolk sac anymore, although there were individuals having visible remnants left inside their body walls (e.g. Garcia de Leaniz *et al.* 2000, Skoglund & Barlaub 2006), but it is possible that all fry were not even emerged yet from the gravel due to the potential variation in actual spawning time (Fleming 1996).

On the other hand, both the relative importance of dominant substrate size and the lack of spatial associations imply that these areas with coarse gravel-cobble substrates are very important for a successful dispersion of newly emerged fry, by providing suitable microhabitats (Gustafson-Greenwood & Moring 1990, Nislow *et al.* 1999, 2000, Garcia de Leaniz *et al.* 2000) at larger distances for “drifting” fry (e.g. Bujold *et al.* 2004) as well and thus also potentially reduce the effects of early density-dependent mechanisms, such as mortality caused by exclusion from suitable near-redd habitats. For example, Garcia de Leaniz *et al.* (2000) found that newly emerged dispersed fry were mostly found in riffle-type microhabitats.

4.2. Habitat use and selection of fry in late August

Overall, in the present study, habitat use of fry in late August occurred within similar ranges of single physical habitat variables to those found in numerous previous studies conducted during the summertime (Heggenes *et al.* 1999, Mäki-Petäys *et al.* 2002, 2004, Armstrong *et al.* 2003).

The relative importance of physical habitat variables on the habitat selection of salmon juveniles has varied between previous studies. These differences may arise from several sources, including habitat availability and interaction between variables, different flows and from the scales (i.e. micro- vs. mesohabitat) in which these studies were conducted (e.g. Heggenes 1990, Heggenes & Saltveit 1990, Heggenes *et al.* 1999, Armstrong *et al.* 2003, Finstad *et al.* 2011). For example, DeGraaf & Bain (1986), Morantz *et al.* (1987) and Heggenes & Saltveit (1990) found that the nose velocity, i.e. water velocity measured at the exact position of the snout of fish, was the most important single variable determining habitat selection of juveniles, while Hedger *et al.* (2005) found that depth and substratum size were found to be more important than mean velocity in determining habitat selection of fry at mesohabitat scale. Girard *et al.* (2004) found that only mean water velocity and depth significantly discriminated between the habitat used and not used by fry and this pattern was consistent throughout the summer.

In the present study, mean water velocity was found to be the most important and significant variable affecting habitat selection of fry, although there was a relatively large variation, and most notably two influential points between predicted and observed values,

thus potentially hampering the capability of regression models to detect stronger associations between fry density and water velocity. However, for example, these influential points may possibly be explained by the interaction with depth and substrate which were providing suitable microhabitat niches for fry. It is possible that the coarse substrate in some areas had created suitable lower-velocity niches within areas having generally higher velocities. According to Heggenes (1990), mean water velocity cannot usually be properly separated from substratum in field studies. In the present study, predicted optimum mean water velocity for highest fry density was 0.13 m s^{-1} , which is somewhat lower than those found in previous studies (e.g. Heggenes 1990, Girard *et al.* 2004, Hedger *et al.* 2005), although highest observed densities mostly occurred in areas having slightly faster velocities. However, the range of mean velocities used by fry in the present study was relatively wide, but very similar to those than found in previous studies (e.g. Heggenes 1990, Mäki-Petäys *et al.* 2002, 2004, Hedger *et al.* 2005).

Water depth was also found to be an important variable explaining variation in fry density in late August, although the range of available suitable depths was relatively narrow. The predicted optimum value was approximately 29 cm, which is almost identical to those found by Girard *et al.* (2004) and Hedger *et al.* (2005) (optimum 30 cm for both). Water depth has been found to be more important variable in small streams relative to larger rivers in several previous studies as well, possibly due to the limited availability of suitable depths in small rivers (reviewed by Heggenes 1996). Depth itself combined with surface turbulence may also act as a cover or shelter (e.g. Gibson & Erkinaro 2009).

In the present study, variation in fry density in late August was not related to dominant substrate size. Fry were spread relatively evenly over the range of available substrate sizes, although the observed use occurred mostly within a range of 38–420 mm, i.e. within a coarse gravel-boulder range, which has somewhat larger upper limit than usually has been reported to be used or selected by fry (e.g. Heggenes 1990, Armstrong *et al.* 2003, Mäki-Petäys *et al.* 2002, 2004). It is possible that the dominant substrate size is less precise descriptor of habitat suitability than, for example, composite index of particle sizes. On the other hand, coarser substrate creates habitat complexity by increasing availability of interstitial spaces between particles thus providing shelters and energetically favorable microniches (reviewed by Armstrong *et al.* 2003 and Finstad *et al.* 2011) and it increases visual isolation, which may reduce agonistic intra- and intercohort interactions (e.g. Dolinsek *et al.* 2007, Nislow *et al.* 2011). Indeed, Dolinsek *et al.* (2007) found in their experimental study that added boulders increased salmon population density and that the effect was greatest for age-group 0+ (see also Venter *et al.* 2008). Furthermore, larger particle sizes may also increase for example macroinvertebrate abundance (Allan & Castillo 2007) and thus food availability. Although it is probably too simplistic assumption (for review see Finstad *et al.* 2011), it appears that the overall quality of available substrate sizes, and possibly its heterogeneity created by boulders (e.g. Dolinsek *et al.* 2007, Finstad *et al.* 2007), potentially combined with relatively low intraspecific competition and also reducing this competition (e.g. Venter *et al.* 2008, Nislow *et al.* 2011) was mostly providing optimal conditions or at least tolerable ranges (Morantz *et al.* 1987) for fry, thus acting as a non-limiting resource. Consequently, other factors were found to be relatively more important in determining the habitat selection of fry.

It is also possible that due to the near allopatric conditions in the study area, i.e. due to low competition and more notably low predation risk caused by brown trout and probably by other instream predators, water depth itself (e.g. Gibson & Erkinaro 2009) and surface turbulence as a function of water velocity (reviewed by Heggenes *et al.* 1999) may

also have been relatively more important by providing cover and shelter from other predators such as fish-foraging birds (e.g. Dionne & Dodson 2002).

In addition to the potential effects of interaction between physical variables, it is possible that the overall range of habitats used by fry may also partly reflect the near allopatric conditions in the study area. Although juvenile salmon live in sympatry with brown trout in the River Akujoki, the low abundance of brown trout observed in this study and in the yearly electrofishing assessment of the River Akujoki (FGFRI, unpublished data) suggest that the overall effect of interspecific competition on habitat selection and use of fry could be considered almost negligible. Brown trout has been found to be aggressive and dominant to salmon of similar size (e.g. Harwood *et al.* 2002, Höjesjö *et al.* 2005, Gibson & Erkinaro 2009) and in sympatry juvenile salmon has been found to utilize faster flowing and shallower habitats than trout (reviewed by Heggenes *et al.* 1999). In the absence of brown trout salmon fry may use a wider range of habitat types than in sympatry (reviewed by Heggenes 1990, Heggenes *et al.* 1999). For example, Kennedy & Strange (1986) found that in near allopatric conditions (trout were removed from the study area prior to salmon stocking) salmon fry changed their distribution over the entire available habitat, including also deeper areas, and shallow and fast-flowing areas became the least selected habitat.

In the present study, more than 25 % of the explained variation in fry density was related to distance from spawning redds (or 10.4 % of the total variation if the effect of other factors were controlled for) to distance from spawning redds in late August, approximately more than 8 weeks after the emergence of fry, although the observed redds were located relatively evenly throughout the study area. Moreover, variation in fry density was slightly heterogenous in relation to distance from redds, thus potentially suggesting that the distance may have acted more effectively as a maximum limiting factor than as a determinant of habitat selection of fry. Foldvik *et al.* (2010) found that 21 % of the spatial variation in fry density along the entire reach (9.2 km) of the Norwegian River Vigda was attributed to the spatial variation in spawning redd distribution approximately 5–7 weeks after the emergence. Teichert *et al.* (2011) found that the distribution of spawning sites with the amount of nest area being the most important correlate of local fry densities in a 3.1 km long section of the River Borsa in July, and physical habitat had a little effect on observed fry density.

In the present study, only spawning redd locations, i.e. either a single redd or a cluster of redds without any further quantification was considered as a single source for egg deposition, while in the two above-mentioned studies the total redd/nest area at each site was used as a proxy for egg deposition, which is more accurate estimate of the total egg deposition (Foldvik *et al.* 2010, Teichert *et al.* 2011). Also, larger females have a larger number of eggs and they tend to dig larger redds (e.g. Crisp & Carling 1989). However, the spawning population in the River Akujoki is dominated by 1SW fish, and only six 2SW females (14 % from the estimated total number of female spawners) were observed in the study area prior to the spawning period in 2006 (Panu Orell, unpublished data). On the other hand, larger females may have more tendency to dig several redds than just one, when compared to smaller females, and redds may be located several hundred meters or even up to few kilometers from each other (Taggart *et al.* 2001). Furthermore, it has been shown that due to locally high egg deposition and limited early dispersal of fry, the local carrying capacity is often exceeded close to the spawning site and as a consequence, density-dependent mortality rates are high during the subsequent post-emergence period within the following few weeks (Nislow *et al.* 2004, Einum & Nislow 2005). During this early critical period, mortality rates ranging from approximately 60 to

95 % have been observed (Nislow *et al.* 2004). Einum & Nislow (2005) found in their experimental study that the level of mortality during this period was inversely related to density of hatched eggs per nest and they also found that the following dispersal rates of emerging juveniles were only weakly related to nest size. In contrast, Einum *et al.* (2006) found in their manipulative study that dispersal of reared fry released 2–3 months after onset of their feeding was strongly density-dependent, with more individuals emigrating from high-density release sites, although this dispersal was not sufficient enough to produce an ideal free distribution within the study stream. However, as noted by Einum *et al.* (2008), their results were based on hatchery-reared and outplanted fry at predetermined densities as older fish, and this situation may differ from natural conditions due to the behavioral differences and the excluded effect of early density-dependent processes. All these above mentioned factors may partly weaken the expected direct relationship between high local egg deposition and high subsequent fry abundance near redds later during the summer.

In the present study, spawning redd survey took place almost immediately after the main spawning activity had ceased. Thus, it is likely that there may have been some late individual spawners and consequently their redds were ignored. However, it is also possible that these fish may have dug their redds in the same areas as those which were observed, thus also potentially resulting in superimposition of redds (e.g. Taggart *et al.* 2001). It is also possible that divers did not observe all redds.

Nevertheless, considering the relatively uniform distribution of redd areas observed in the study area, and the overall good habitat suitability as well, there still was a considerable amount of variation in fry density in relation to spatial spawning redd distribution approximately two months after the emergence. Thus, this result from the present study also supports previous findings (Foldvik *et al.* 2010, Teichert *et al.* 2011) that not only the habitat quality and active selection of available habitats but also the spatial distribution of spawning areas or female breeders is an important mechanism that affects habitat selection of Atlantic salmon fry in the wild and creates variation in population density at small spatial scales.

4.3. Effect of parr density

In the present study, fry density was not related to parr density either in early July or in late August. Assuming that the mean catchability would have been for both fry and parr approximately the same as in the assessment data for fry (0.58), this would correspond to estimated mean density (of 100m² in area) 8.4 for fry (max 46.1) and 46.8 (max 147.9) for parr per transect in early July (two outliers removed). In late August, estimated mean densities (of 100m² in area) would have been 35.4 for fry (max 68.3) and 44.8 for parr (max 128.0) per transect. In the present study, it was usual to catch juveniles from several age groups with total lengths varying from 30 to 125 mm within a single transect. Territory size is commonly related to fish size, with observed mean size varying, for example, from 0.5 m² for fry (55 mm in fork length) to 1.14 m² for parr (114 mm in fork length) (Symons 1971, Cutts *et al.* 1999). It may be so that the overall abundance of juveniles was too low and it would have required more individuals to exist per transect for territorial intercohort interactions to have larger role and to cause exclusion of fry from preferred habitats. Therefore, due to the relatively low overall abundance, it is possible that the expected intercohort competition may have acted more via exploitation (e.g. depletion of food by competitors) or via other interference competition mechanisms such as shadow competition (where dominant individual has first access to the resource, e.g. Elliott 2002) within a habitat than via territoriality causing interactions such as emigration or exclusion

from preferred habitats (reviewed by Grant & Imre 2005, Nislow *et al.* 2011). Interestingly, Teichert *et al.* (2011) found in their field study that parr density was positively related to fry density. However, due to the expected antagonistic relationship between cohorts, they concluded that this phenomenon would have been caused by the fact that certain habitats simply attracted larger numbers of parr within the study area or that parr were remained close their native sites thus resulting this positive correlation between cohorts (Teichert *et al.* 2011).

In addition to more or less different age- and size related habitat requirements, it has been shown in previous studies that different age-groups may also differ in their resource use and behaviour, for example in feeding strategies and in use of feeding habitats: parr may have seasonal shifts in their feeding activity, while fry may increase their feeding throughout the summer to continue their growth (Grader & Letcher 2006, Kennedy *et al.* 2008). Newly emerged fry tend to feed on small prey, whereas larger juveniles tend to select larger prey than average available (Keeley & Grant 1997). Both fry and parr feed from the drift, but parr and especially larger parr tend to feed more frequently from the surface (reviewed by Johansen *et al.* 2011) while fry may feed more frequently from the benthos (Nislow *et al.* 1998). It is also possible that strict territorial behaviour may not always hold in all situations. For example, Armstrong *et al.* (1999) found that despite aggressive interactions and dominant behavior between parr of similar sizes, fish showed a high level of space sharing with considerable overlap of home ranges and adopted different feeding strategies. Also, Økland *et al.* (2004) found that larger parr (113–178 mm in length) used habitats in a flexible manner: fish were shoaling and forming hierarchies instead of defending fixed territories. Moreover, Lindeman *et al.* (2014) found in their recent experimental study that territory size of fry decreased with increasing density. These factors may potentially reduce the strength of expected intra- and intercohort competitive interactions.

It is also possible that other unmeasured factors such as food abundance and habitat heterogeneity (for example, physical shelters and visual isolation created by boulders, e.g. Dolinsek *et al.* 2007) and near allopatric conditions and probably low predation risk may have reduced the competition for space both within and between cohorts. Territory size has been found to be inversely related to habitat heterogeneity (e.g. Dolinsek *et al.* 2007, Venter *et al.* 2008) and to food availability, although with relatively moderate effects (Keeley & Grant 1995, Steingrimsson & Grant 1999 and references therein). On the other hand, both lack of predators and increased food abundance may increase aggressive interactions on a short term basis (Vehanen 2003).

However, the observed insignificant effect of parr density on habitat selection on fry was based on among transect comparison thus reflecting the realized niche. Therefore, it is also possible that especially the observed low abundance of fry at transects in early July was not only a result of limited dispersal or narrow ontogenetic requirements (e.g. Heggenes & Traaen 1988, Nislow *et al.* 1999, 2000) of newly emerged fry, but it is also possible that this low abundance may partly have been caused by intercohort exclusion from these habitats. For example, Kaspersson *et al.* (2012) found in their manipulative experimental study that in the absence of older juveniles, age-0 trout selected habitats that were located further from their nursery habitats. Hence, in the present study, the important question (e.g. Armstrong & Nislow 2006), whether this low abundance reflected only size-related requirements or also exclusion from preferred habitats, remained unsolved. It is also important to note that in the present study also parr densities were estimated by single-pass electrofishing. Therefore, it is possible that measurement error in independent variable, i.e. in parr density indices, may have caused some bias, i.e. regression dilution in

regression models (e.g. Quinn & Keough 2002). Consequently, these insignificant relationships between fry and parr densities should be treated with some skepticism.

4.4. Habitat suitability index values vs. direct measurements

Results obtained from the models fitted with suitability index values were similar to those fitted with direct measurements, and the same corresponding suitability index variables had the best predictive capability in all four cases. However, in early July, substrate suitability index value had clearly weaker explanatory power than the model fitted with direct measurements. As noted earlier, innate requirements of Atlantic salmon fry change (e.g. Heggenes & Traaen 1988) shortly after the emergence and they undergo ontogenetic niche shift during the first summer (e.g. Nislow *et al.* 1999, 2000). Thus, it is possible that the data obtained and merged from several studies were collected several weeks after the emergence of fry in these particular rivers, and therefore these suitability curves (Heggenes 1990 and references therein, Mäki-Petäys *et al.* 2002) most likely represent habitat suitability values for later ontogenetic stages of fry. Consequently, this difference in timing may explain the weaker explanatory capability of this model. Nevertheless, in both cases results were similar: the dominant substrate size and its corresponding suitability index value were the only significant predictors of fry density variation shortly after the emergence of fry.

In late August, the final model fitted with suitability index values for depth and water velocity had nearly the same explanatory power than the model fitted with habitat measurements, if the effect of distance variable was removed from the models. Obviously, the relationship between fry density and suitability index values for dominant substrate size in late August suggests that the generalized suitability index data for substrate size were not “transferable” to this study, caused by the substrate availability and possibly by its heterogeneity.

As noted earlier, variation in density was often more or less heterogeneous in relation to values of individual habitat variables and these patterns were also clearly shown with the suitability index models. Considering these patterns and the similarity between the results obtained from measurement and index models, and despite the other potential effects, such as differences in habitat availability (e.g. Heggenes 1990) or in biotic interactions (e.g. Mäki-Petäys *et al.* 1999) or scales (e.g. micro- vs. mesohabitat, e.g. Heggenes *et al.* 1999) and methods applied (Heggenes *et al.* 1999) between the present study and the rivers from which these data were obtained (Heggenes 1990 and references therein), it can be inferred that the generalized suitability criteria obtained from suitability curves themselves for both water depth and velocity were probably sufficient enough and thus “transferable” to this study. However, both direct measurements and suitability index values had poor explanatory power and thus the major problem for both approaches in their capability to predict variation in fry abundance was most likely a methodological one or hampered by their interaction with other, unmeasured variables. As emphasized by Mäki-Petäys *et al.* (1999), when habitat index data are used for predictive purposes, underlying “bottlenecks” should be identified.

4.5. Sources of errors and uncertainty

In the present study, most of the variation in fry densities remained unexplained. It is important to consider the effects of errors incorporated in the study design and applied methods, which may have prevented to detect deeper associations in the habitat-abundance relationships.

Firstly, in this study, juvenile density data were obtained by single-pass electrofishing, which is a commonly used approach in fish-habitat studies and in fish stock assessments (e.g. Kruse *et al.* 1998, Bateman *et al.* 2005, Hedger *et al.* 2005 and references therein), but it is less precise than multiple-pass methods. Considering the data from the yearly electrofishing assessment of the River Akujoki, which were obtained from the same area and under similar prevailing environmental conditions, it is reasonable to assume that the average relative precision of single-pass results in these data would apply to this study as well. In these data, first-pass results explained, on average, 87 % of the variation in fry density compared to three-pass estimates and the average amount of relative error was 16 %. Furthermore, there was no visually apparent systematic bias between single-pass results and three-pass estimates. From the statistical point of view, it should be noted that if the measurement error in dependent variable is a random one, it does not bias the estimate itself, but it causes inability to estimate relationships precisely due to large variances, i.e. random error increases both the unexplained and unexplainable part of regression models (e.g. Quinn & Keough 2002). However, three-pass method is also prone to noise, i.e. to random errors (Bohlin *et al.* 1989). The relative precision of three-pass estimates in the River Akujoki electrofishing assessment data was on average 11.6 %, which, (*sensu* Bohlin *et al.* 1989), should be approximately enough to detect a density change of a factor of 1.6 in space in 95 cases out of 100. This is in practical terms, for example, a decrease from 20 to 13 or an increase from 20 to 32 fish per 100m² in “true” estimated population sizes between individual estimates (Bohlin *et al.* 1989). Therefore, it is reasonable to assume that in the present study, the unexplained variation in fry densities was not caused by the random error of single-pass electrofishing alone.

Secondly, as noted earlier, it is obvious that the too coarse spatial resolution in the study design, combined with too early timing most likely prevented the detection of any spatial associations between spawning redds and fry abundance in early July. It is also important to consider the potential effects of resolution at within site scale as well. Both abundance of organisms and levels of physical variables may be heterogeneous at relatively small scales in rivers (e.g. Lancaster & Belyea 2006 and references therein) and in the present study, due to the sample design, cross-river -transects represented relatively coarse and heterogeneous mesohabitats, which may have reduced the capability to detect important relationships between fry density and explanatory variables, especially during the first survey. On the other hand, transects may have been too narrow, probably causing variation in densities due to short term fish movements (Bouchard & Boisclair 2008).

Thirdly, ordinary least square regression methods are often very sensitive to even a single outlier or an influential point and the basic requirements of these methods are easily violated (e.g. Quinn & Keough 2002, Torgersen *et al.* 2012). In the present study, the number of samples was relatively low and especially the ratio of samples per explanatory variables was low thus potentially causing uncertainty to models. It is possible that due to statistical uncertainty and large variation in densities in relation to explanatory variables, some of the important variables may have been excluded from the final models thus leading to the erroneous conclusion that these variables were unimportant in determining habitat selection of fry (e.g. Dunham *et al.* 2002, Armstrong *et al.* 2003). For example, there were a large number of zero observations in the first survey data, thus causing heteroscedasticity in the models, but these patterns were not improved even after data transformations. Consequently this, for example, may have caused the rejection of water velocity from the final models. Correlative methods, such as ordinary least square regression methods are typically ineffective for noisy data and when strong correlations between independent and dependent variables are lacking (e.g. Torgersen *et al.* 2012), and

interaction between independent variables further complicates interpretation (e.g. Armstrong *et al.* 2003). In fish-habitat studies, alternative methods, such as discriminant analysis (e.g. Heggenes & Saltveit 1990) or more advanced regression methods, such as logistic regression (e.g. Girard *et al.* 2004) are often used to identify important variables. Non-parametric models, such as generalized additive models (e.g. Hedger *et al.* 2005, Teichert *et al.* 2011) are often used, or more traditionally data are transformed, for example log-transformed, to reduce the noise that typically occurs in habitat-abundance data (e.g. Dunham *et al.* 2002).

4.6. Main findings of the study

Overall, habitat use of salmon fry in the present study occurred within similar ranges in relation to physical habitat variables as found in numerous previous studies (for reviews, see Heggenes 1990, Heggenes *et al.* 1999, Armstrong *et al.* 2003). Final models predicted density increase within similar ranges and with more or less similar optimum values in relation to single physical habitat variables or to combination of variables as found in many previous studies (e.g. Girard *et al.* 2004, Hedger *et al.* 2005) or as would have been expected from developed habitat suitability curves (Heggenes 1990, Scruton & Gibson 1993, Mäki-Petäys *et al.* 2002, 2004). These relationships were also more or less present in some other, but statistically non-significant relationships between fry density and explanatory variables. For example, despite the variation in density, the observed habitat use of fry occurred almost exclusively within the range of optimum suitability values for depth in early July.

Previous studies have shown that age-0+ salmon undergo seasonal changes in their habitat use (Heggenes & Saltveit 1990, Mäki-Petäys *et al.* 2004) and also ontogenetic shift during the first summer (e.g. Nislow *et al.* 1999, 2000) and the dispersal of fry has been typically mostly very limited during the first few weeks after the emergence (e.g. Beall *et al.* 1994, Garcia de Leaniz *et al.* 2000, Webb *et al.* 2001, Bujold *et al.* 2004, Einum & Nislow 2005, Einum *et al.* 2008). These patterns were apparent in the present study as well. Compared to early July, fry were more dispersed and had a considerably wider spatial niche exhibiting a change in the observed habitat use in relation to physical habitat variables, especially in relation to dominant substrate size, during the latter survey in late August.

Perhaps the main finding of the present study was that although it was possible to find, in a broad sense, those habitats that were selected by fry, there was a large variation in density between individual sites and this variation often increased as the predicted optimality for a certain habitat variable or combination of variables increased. These patterns in fry abundance were similar to those that were found by Hedger *et al.* (2005). In the present study, similar heterogeneous patterns were also often more or less present in some statistically non-significant relationships between fry abundance and a certain variable, for example shown in the density-velocity scatterplot in early July. When considering the relationships between individual explanatory variables and fry abundance, it is obvious that some of this variation was attributed to the interaction with other variables. For example, in late August, relatively high densities were found in transects having only suboptimal suitability value for water velocity, possibly caused by heterogeneous substrate providing suitable low-velocity niches. It is also possible that the overall good habitat availability, as the most of transects provided at least suboptimum suitability values for fry, may have prevented the detection of deeper associations between abundance and physical habitat characteristics. As noted by Shirwell (1989, cited in Mäki-Petäys *et al.* 1999) habitat models can be expected to correlate closely with abundance

only if a species' tolerable range for a certain habitat variable is exceeded. However, in the present study, despite the narrow ranges of available habitats, in some cases clear patterns of habitat selection still existed in relation to certain variables. For example, in late August, although almost all (91 %) transects provided optimum depth suitability index values for fry, the suitability index value for depth still explained considerable amount of the variation in fry density, possibly due to the limited availability of suitable depths (e.g. Heggenes 1996) in the study area. On the other hand, in the present study, habitat selection of fry in late August was confounded by available dominant substrate sizes, possibly suggesting that habitat heterogeneity (e.g. Dolinsek *et al.* 2007, Finstad *et al.* 2007) created by larger particles was a non-limiting or "uncontested" (Garshelis 2000, cited in Railsback *et al.* 2003) resource for fry.

Despite the potential effects of sampling errors, statistical and structural uncertainty and interactions between measured variables, it is important to note that in the present study the observed variation in fry density was often heterogeneous in relation to explanatory variables. Similar "factor-ceiling" (Thomson *et al.* 1996) or "wedge-shaped" patterns (Terrell *et al.* 1996) of responses to environmental predictors with weak explanatory power of models have been found in many previous salmonid abundance-habitat studies (e.g. Terrell *et al.* 1996, Dunham *et al.* 2002, Hedger *et al.* 2005, Torgersen *et al.* 2012 and references therein) and it has been a common phenomenon in many ecological abundance-habitat field studies as well (for discussion, see Thomson *et al.* 1996, Cade *et al.* 1999, Lancaster & Belyea 2006). Thus, it can be inferred that these patterns observed in the present study suggest that the abundance of fry was influenced by other, but unmeasured factors as well. As reviewed in the introduction part of the present study, abundance and distribution of juvenile Atlantic salmon in rivers are influenced by multiple factors simultaneously, but many of these factors are often unmeasured (e.g. Armstrong *et al.* 2003).

It is possible that factors such as food availability (e.g. Vehanen 2003), individual variability in preferences and behaviour (Heggenes *et al.* 1999, Roy *et al.* 2013), intracohort competition (e.g. Bult *et al.* 1999) and territoriality (e.g. Grant *et al.* 1998), low interspecific competition and potentially low predation risk, habitat heterogeneity (e.g. Dolinsek *et al.* 2007, Venter *et al.* 2008) and habitat discontinuity (Railsback *et al.* 2003) may have affected the habitat use and selection of fry. Additionally, it is probable that intercohort exclusion from preferred habitats (Kaspersson *et al.* 2012) and the "limited habitat knowledge" (Railsback *et al.* 2003) created for example, by longer pools, may have affected the dispersion of fry. It is also possible that there have been short-term behavioral responses to transitory events, which may have affected the observed densities, for example to variation in food abundance (Vehanen 2003). Furthermore, it is also possible that the occurrence of low-density areas within optimal habitats was partly caused by the relatively overall low abundance of fry.

In the present study, it was hypothesized that abundance of fry would primarily respond to chosen explanatory variables and these relationships were consequently modeled with regression analysis, i.e. with such a method that describes the central tendency of the response as a function of predictor variables (e.g. Cade *et al.* 1999, Lancaster & Belyea 2006). According to the basic ecological principle, the law of limiting factors, although several factors can potentially limit for example, abundance of fish, not all of them will be the active constraint at all places or times (e.g. Cade *et al.* 1999, Dunham *et al.* 2002). As emphasized by Thomson *et al.* (1996), there is a fundamental conflict between the basic ecological concept of limiting factors and correlative methods. An alternative view (*sensu* Lancaster & Belyea 2006) in the present study would have been

to consider these relationships as limiting responses, thus acknowledging that certain measured physical habitat variables, for example depth and velocity, may have acted more as minimum and maximum limits of abundance (see also Thomson *et al.* 1996, Cade *et al.* 1999) and some other, but unmeasured factor within these limits defined the observed realized niche and consequently model these relationships with quantile regression models. However, as reviewed earlier, unequal variation is often treated as unwanted noise in habitat studies, although this variation may also indeed provide important ecological information (e.g. Lancaster & Belyea 2006). In the present study, for example, unequal variation exhibiting a “wedge-shaped” pattern in the parr density–fry density scatterplot in late August suggests that there possibly was an inverse relationship between these variables, and thus potentially upper limit for habitat selection of fry in relation to parr abundance, although the overall effect as a “central tendency” (Lancaster & Belyea 2006) was not revealed by the linear regression model.

Perhaps the most interesting single finding in this study was the effect of spatial spawning redd distribution on fry density in late August. Considering the relatively uniform spatial dispersion of redd areas observed in the short study section and the overall good habitat suitability, and also the timing of survey, approximately two months after the emergence of fry, there still was a considerable amount of variation in fry density in relation to spatial spawning redd distribution. Although this result was based on only one subpopulation and from one year, this finding is backed-up by the results from several experimental studies (e.g. Crisp 1995, Einum & Nislow 2005, Einum *et al.* 2008) and from two studies (Foldvik *et al.* 2010, Teichert *et al.* 2011) conducted in natural populations. Thus, this result from the present study also supports the view that not only the habitat quality and active selection of available habitats, but also the spatial distribution of spawning areas and female breeders is an important mechanism that affects habitat selection of Atlantic salmon fry in the wild and creates variation in population density at small scales. Consequently, as noted by Foldvik *et al.* (2010) and Teichert *et al.* (2011) spatial spawning distribution influences juvenile abundance via density-dependent mortality and growth of fry and thus potentially influences population carrying capacity.

4.7. Conclusions and recommendations

Despite the fact that the results of the present study were obtained from only one subpopulation and from one-year data, it is suggested that the future habitat studies of Atlantic salmon juveniles under similar conditions may potentially benefit from considering physical habitat variables more as limiting edges than determinants of abundance and consequently take this difference also into account when applying statistical methods. Alternatively or additionally, it would be useful to focus on the importance of other, but often unmeasured factors that may affect juvenile salmon abundance and also focus on the interaction between different factors.

These results also suggest, as found in previous studies, that at least in some cases, generalized habitat suitability criteria themselves may be sufficient enough for at least crude predictive purposes, and the major problem often associated to habitat suitability criteria is not always necessarily in its universality or transferability between rivers, but this problem may also be methodological.

Most importantly, in addition to results obtained from previous experimental and field studies, results from the present study also support the view that the spatial spawning distribution may be an important mechanism that affects Atlantic salmon juvenile production.

ACKNOWLEDGMENTS

I greatly appreciate all the support and advice from my supervisors Panu Orell and Timo J. Marjomäki. Joonas Isoketo and Joonas Ikonen from the Department of Mathematics and Statistics of JYU provided invaluable help with statistical modelling. I am grateful to the field personnel: Ville Kangasniemi, Ossi Käkränen and Panu Orell's diving team, whose efforts made this study possible. I would also like to thank Juha-Pekka Vähä, Jorma Kuusela and Aki Mäki-Petäys for providing additional data and help.

REFERENCES

- Allan J.D. & Castillo M.M. *Stream ecology. Structure and function of running waters*. 2nd ed. Springer, Dordrecht, Netherlands.
- Armstrong J.D. & Nislow K.H. 2006. Critical habitat during the transition from maternal provisioning in freshwater fish, with emphasis on Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*). *J. Zool.* 269: 403–413.
- Armstrong J.D., Huntingford F.A. & Herbert N.A. 1999. Individual space use strategies of wild juvenile Atlantic salmon. *J. Fish Biol.* 55: 1201–1212.
- Armstrong J.D., Kemp P.S., Kennedy G.J.A., Ladle M., & Milner N.J. 2003. Habitat requirements of Atlantic salmon and brown trout in rivers and streams. *Fish. Res.* 62: 143–170.
- Ayllón D., Nicola G.G., Parra I., Elvira B. & Almodóvar A. 2013. Intercohort density dependence drives brown trout habitat selection. *Acta Oecol.* 46: 1–9.
- Bardonnet A. & Baglinière J.L. 2000. Freshwater habitat of Atlantic salmon (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* 57: 497–506.
- Bateman D.S., Gresswell R.E. & Torgersen C.E. 2005. Evaluating single-pass catch as a tool for identifying spatial pattern in fish distribution. 2005. *J. Freshw. Ecol.* 20: 335–345.
- Beall E., Dumas J., Claireaux D., Barriere L. & Marty C. 1994. Dispersal patterns and survival of Atlantic salmon (*Salmo salar* L) juveniles in a nursery stream. *ICES J. Mar. Sci.* 51: 1–9.
- Bohlin T., Hamrin S., Heggberget T.G., Rasmussen G. & Saltveit S.J. 1989. Electrofishing — theory and practice with special emphasis on salmonids. *Hydrobiologia* 1731: 9–43.
- Bouchard J. & Boisclair D. 2008. The relative importance of local, lateral, and longitudinal variables on the development of habitat quality models for a river. *Can. J. Fish. Aquat. Sci.* 65: 61–73.
- Bovee K.D. 1986. Development and evaluation of habitat suitability criteria for use in the instream flow incremental methodology. Instream Flow Information Paper 21. *U.S. Fish Wildl. Serv. Biol. Rep.* 86 (7): 1–235.
- Bremset G. & Berg O.K. 1999. Three-dimensional microhabitat use and preferences by young pool-dwelling Atlantic salmon and brown trout. *Anim. Behav.* 58: 1047–1059.
- Bryant M.D., Caquette J.P. & Wright B. E. 2004. Evaluating habitat survey data and statistical power using an example from Southeast Alaska. *N. Am. J. Fish. Manage.* 24: 1353–1362.
- Bujold V., Cunjak R.A., Diertrich J.P. & Courtemanche D.A. 2004. Drifters versus residents: assessing size and age differences in Atlantic salmon (*Salmo salar*) fry. *Can. J. Fish. Aquat. Sci.* 61: 273–282.
- Bult T.P., Riley S.C., Haedrich R.L., Gibson R.J. & Heggenes J. 1999. Density dependent habitat selection by juvenile Atlantic salmon (*Salmo salar*) in experimental riverine habitats. *Can. J. Fish. Aquat. Sci.* 56: 1298–1306.
- Cade B.S., Terrell J.W. & Schroeder R.L. 1999. Estimating effects of limiting factors with regression quantiles. *Ecology* 80: 311–323.

- Crisp D.T. 1995. Dispersal and growth rate of 0-group salmon (*Salmo salar* L.) from point stocking together with some information from scatter-stocking. *Ecol. Freshw. Fish* 4: 1–8.
- Crisp D.T. & Carling P.A. 1989. Observations on siting, dimensions and structure of salmonid redds. *J. Fish Biol.* 34: 119–134.
- Cutts C.J., Brembs B., Metcalfe N.B. & Taylor A.C. 1999. Prior residence, territory quality and life-history strategies in juvenile Atlantic salmon (*Salmo salar* L.). *J. Fish Biol.* 55: 784–794.
- DeGraaf D.A. & Bain L.H. 1986. Habitat use and preferences of juvenile Atlantic salmon in two Newfoundland Rivers. *Trans. Am. Fish. Soc.* 115: 671–681.
- Dionne M. & Dodson J.J. 2002. Impact of exposure to a simulated predator (*Mergus merganser*) on the activity of juvenile Atlantic salmon (*Salmo salar*) in a natural environment. *Can. J. Zool.* 80: 2006–2013.
- Dolinsek I.J., Grant J.W.A. & Biron P.M. 2007. The effect of habitat heterogeneity on the population density of juvenile Atlantic salmon *Salmo salar* L. *J. Fish Biol.* 70: 206–214.
- Dunham J.B., Cade B.S. & Terrell J.W. 2002. Influences of spatial and temporal variation on fish–habitat relationships defined by regression quantiles. *Trans. Am. Fish. Soc.* 131: 86–98.
- Einum S. & Kvingedal E. 2011. Relative importance of size-based competitive ability and degree of niche overlap in inter-cohort competition of Atlantic salmon (*Salmo salar*) juveniles. *Can. J. Fish. Aquat. Sci.* 68: 1–8.
- Einum S. & Nislow K.H. 2005. Local-scale density-dependent survival of mobile organisms in continuous habitats: an experimental test using Atlantic salmon. *Oecologia* 143: 203–210.
- Einum S. & Nislow K.H. 2011. Variation in population size through time and space: theory and recent empirical advances from Atlantic salmon. In: Aas Ø., Einum S., Klemetsen A. & Skurdal J. (eds.), *Atlantic Salmon Ecology*. Blackwell Publishing Ltd, Oxford, pp. 277–298.
- Einum S., Sundt-Hansen L. & Nislow K.H. 2006. The partitioning of density-dependent dispersal, growth and survival throughout ontogeny in a highly fecund organism. *Oikos* 113: 489–496.
- Einum S., Nislow K.H., McKelvey S. & Armstrong J.D. 2008. Nest distribution shaping within-stream variation in Atlantic salmon juvenile abundance and competition over small spatial scales. *J. Anim. Ecol.* 77: 167–172.
- Einum S., Robertsen G., Nislow K.H., McKelvey S. & Armstrong J.D. 2011. The spatial scale of density-dependent growth and implications for dispersal from nests in juvenile Atlantic salmon. *Oecologia*. 165: 959–969.
- Elliott J.M. 2002. Shadow competition in wild juvenile sea trout. *J. Fish Biol.* 61: 1268–1281.
- Erkinaro J., Dempson J.B., Julkunen M. & Niemelä E. 1997. Importance of ontogenetic habitat shifts to juvenile output and life history of Atlantic salmon in a large subarctic river: an approach based on analysis of scale characteristics. *J. Fish Biol.* 51: 1174–1185.
- Fausch K.D. 1998. Interspecific competition and juvenile Atlantic salmon (*Salmo salar*): on testing effects and evaluating the evidence across scales. *Can. J. Fish. Aquat. Sci.* 55: 218–231.
- Fausch K.D., Hawks C.L. & Parsons M. G. 1988. Models that predict standing crop of stream fish from habitat variables: 1950–85. *USDA Forest Service Gen. Tech. Rep. PNW-GTR-213*: 1–52.
- Fausch K.D., Torgersen C.E., Baxter C.W. & Li H.W. 2002. Landscapes to riverscapes: Bridging the gap between research and conservation of stream fishes. *BioScience* 52: 483–498.
- Finstad A.G., Armstrong J.D. & Nislow K.H. 2011. Freshwater habitat requirements of Atlantic salmon. In: Aas Q, Einum S., Klemetsen A. & Skurdal S. (eds.), *Atlantic Salmon Ecology*. Blackwell Publishing Ltd., Oxford, pp. 67–87.

- Finstad A.G., Einum S., Forseth T. & Ugedal O. 2007. Shelter availability affects behaviour, size-dependent and mean growth of juvenile Atlantic salmon. *Freshwat. Biol.* 52: 1710–1718.
- Finstad A.G., Einum S., Sættem L.M. & Hellen B.A. 2010. Spatial distribution of Atlantic salmon breeders: among- and within-river variation and predicted consequences for offspring habitat availability. *Can. J. Fish. Aquat. Sci.* 67: 1993–2001.
- Fleming I.A. 1996. Reproductive strategies of Atlantic salmon: ecology and evolution. *Rew. Fish. Biol. Fisher.* 6: 379–416.
- Fleming I.A. & Einum S. 2011. Reproductive ecology: a tale of two sexes. In: Aas Ø., Einum S., Klemetsen A. & Skurdal J. (eds.), *Atlantic Salmon Ecology*. Blackwell Publishing Ltd, Oxford, pp. 33–65.
- Foldvik A., Finstad A.G. & Einum S. 2010. Relating juvenile spatial distribution to breeding patterns in anadromous salmonid populations. *J. Anim. Ecol.* 79: 501–509.
- Fretwell S.D. 1972. *Populations in a Seasonal Environment*. Princeton University Press, Princeton, New Jersey.
- Fretwell S.D. & Lucas H.L. 1970. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheor.* 19: 16–36.
- Garcia de Leaniz C., Fraser N. & Huntingford F.A. 2000. Variability in performance in wild Atlantic salmon, *Salmo salar* L., fry from a single redd. *Fish. Manag. Ecol.* 7: 489–502.
- Gibson A.J.F., Bowby H.D. & Amiro P.G. 2008. Are wild populations ideally distributed? Variations in density-dependent habitat use by age class in juvenile Atlantic salmon (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* 65: 1667–1680.
- Gibson R.J. 1993. The Atlantic salmon in fresh water: spawning, rearing and production. *Rew. Fish. Biol. Fisher.* 3: 39–73.
- Gibson R.J. & Erkinaro J. 2009. The influence of water depths and inter-specific interactions on cover responses of juvenile Atlantic salmon. *Ecol. Freshw. Fish* 18: 629–639
- Girard I., Grant J.W.A. & Steingrímsson S.O. 2004. Foraging, growth and loss rate of young-of-the-year Atlantic salmon (*Salmo salar*) in relation to habitat use in Catamaran Brook, New Brunswick. *Can. J. Fish. Aquat. Sci.* 61: 2339–2349.
- Grader M. & Letcher B.H. 2006. Diel and Seasonal Variation in Food habits of Atlantic Salmon Parr in a Small Stream. *J. Freshw. Ecol.* 21: 503–517.
- Grant J.W.A. & Imre I. 2005. Patterns of density-dependent growth in juvenile stream-dwelling salmonids. *J. Fish Biol.* 67: 100–110.
- Grant J.W.A., Steingrímsson S.O., Keeley E.R. & Cunjak R.A. 1998. Implications of territory size for the measurement and prediction of salmonid abundance in streams. *Can. J. Fish. Aquat. Sci.* 55: 181–190.
- Guay J.C., Boisclair D., Leclerc M. & Lapointe M. 2003. Assessment of the transferability of biological habitat models for Atlantic salmon parr (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* 60: 1398–1408.
- Guay J.C., Boisclair D., Rioux D., Leclerc M., Lapointe M. & Legendre P. 2000. Development and validation of numerical habitat models for juveniles of Atlantic salmon (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* 57: 2065–2075.
- Gustafson-Greenwood K.I. & Moring J.R. 1990. Territory size and distribution of newly-emerged Atlantic salmon (*Salmo salar*). *Hydrobiologia* 206: 125–131.
- Harwood A.J., Armstrong J.D., Griffiths S.W. & Metcalfe N.B. 2002. Sympatric association influences within-species dominance relations among juvenile Atlantic salmon and brown trout *Anim. Behav.* 64: 85–95.

- Harwood A.J., Griffiths S.W., Metcalfe N.B. & Armstrong J.D. 2003. The relative influence of prior residency and dominance on the early feeding behaviour of juvenile Atlantic salmon. *Anim. Behav.* 65: 1141–1149.
- Hedger R.D., Dodson J.J., Bergeron N.E. & Caron F. 2005. Habitat selection by juvenile Atlantic salmon: the interaction between physical habitat and abundance. *J. Fish Biol.* 67: 1054–1071.
- Heggenes J. 1990. Habitat utilization and preferences in juvenile Atlantic salmon (*Salmo salar*) in streams. *Regul. River.* 5: 431–354.
- Heggenes J. 1996. Habitat selection by brown trout (*Salmo trutta*) and Atlantic salmon (*S. salar*) in streams: static and dynamic hydraulic modelling. *Regul. River.* 12: 155–169.
- Heggenes J. & Dokk J.G. 2001. Contrasting temperatures, waterflows, and light: Seasonal habitat selection by young Atlantic salmon and brown trout in a boreonemoral river. *Regul. River.* 17: 623–635.
- Heggenes J. & Saltveit S.J. 1990. Seasonal and spatial microhabitat selection and segregation in young Atlantic salmon, *Salmo salar* L., and brown trout, *Salmo trutta* L., in a Norwegian river. *J. Fish Biol.* 36: 707–720.
- Heggenes J. & Traaen T. 1988. Downstream migration and critical water velocities in stream channels for fry of four salmonid species. *J. Fish Biol.* 32: 717–727.
- Heggenes J., Bagliniere J.L. & Cunjak R.A. 1999. Spatial niche variability for young Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) in heterogeneous streams. *Ecol. Freshw. Fish* 8: 1–21.
- Hutchings J.A. & Jones M.E.B. 1998. Life history variation in growth rate thresholds for maturity in Atlantic salmon. *Can. J. Fish. Aquat. Sci.* 55 (suppl.1): 22–47.
- Hutchinson G.E. 1957. Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology* 22: 415–427.
- Höjesjö J., Armstrong J.D. & Griffiths S.W. 2005. Sneaky feeding by salmon in sympatry with dominant brown trout. *Anim. Behav.* 69: 1037–1041.
- Imre I., Grant J.W.A. & Cunjak R.A. 2005. Density-dependent growth of young-of-the-year Atlantic salmon *Salmo salar* in Catamaran Brook, New Brunswick. *J. Anim. Ecol.* 74:508–516.
- Johansen M., Erkinaro J. & Amundsen P.-A. 2011. The when, what and where of freshwater feeding. In: Aas Ø., Einum S., Klemetsen A. & Skurdal J. (eds.), *Atlantic Salmon Ecology*. Blackwell Publishing Ltd, Oxford, pp. 89–112.
- Johansen M., Erkinaro J., Niemelä E., Heggberget T.G., Svenning M.A. & Brørs S. 2008. *Atlantic salmon monitoring and research in the Tana river system. Outlining a monitoring and research program for the River Tana within the framework of the precautionary approach. Report from the Norwegian-Finnish working group on monitoring and research in Tana.* Available at: http://www.tenojoki.fi/tenopaasivut/arkisto2/final_report_working_group.pdf (05.02.2014).
- Jonsson N., Jonsson B. & Hansen L.P. 1998. The relative role of density dependent and density-independent survival in the life cycle of Atlantic salmon *Salmo salar*. *J. Anim. Ecol.* 67: 751–762.
- Julkunen M., Kuusela J. & Niemelä E. Lohen poikastiheyksien arviointi Tenojoen sähkökalastustuloksista. 1997. In: Julkunen M. & Niemelä E. (eds.), *Sähkökalastus ja sen luotettavuus Tenon lohen poikastiheyksien seurannassa*. Oy Edita Ab, Helsinki, pp. 25–40. [In Finnish with English summary].

- Kaspersson R. 2010. *Age-class interactions in Atlantic salmon and Brown trout: Effects on habitat use and performance*. PhD thesis, University of Gothenburg. Available at: <http://hdl.handle.net/2077/22214> (07.11.2013).
- Kaspersson R. & Höjesjö J. 2009. Density-dependent growth rate in an age-structured population: a field study on stream-dwelling brown trout *Salmo trutta*. *J. Fish Biol.* 74: 2196–2215.
- Kaspersson R., Höjesjö J. & Bohlin T. 2012. Habitat exclusion and reduced growth: a field experiment on the effects of inter-cohort competition in young-of-the-year brown trout. *Oecologia*. 169: 733–742.
- Keeley E.R. & Grant J.W.A. 1995. Allometric and environmental correlates of territory size in juvenile Atlantic salmon (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* 52: 186–196.
- Keeley E.R. & Grant J.W.A. 1997. Allometry of diet selectivity in juvenile Atlantic salmon (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* 54: 1894–1902.
- Kennedy B.P., Nislow K.H. & Folt C.L. 2008. Habitat-mediated foraging limitations drive survival bottlenecks for juvenile salmon. *Ecology* 89: 2529–2541.
- Kennedy G.J.A. & Strange C.D. 1986. The effects of intra- and inter-specific competition on the distribution of stocked juvenile Atlantic salmon, *Salmo salar* L., in relation to depth and gradient in an upland trout, *Salmo trutta* L., stream. *J. Fish Biol.* 29: 199–214.
- Kocik J.F. & Ferreri C.P. 1998. Juvenile production variation in salmonids: population dynamics, habitat, and the role of spatial relationships. *Can. J. Fish. Aquat. Sci.* 55: 191–200.
- Kruse C.G. & Rahel F.J. 1998. Single-Pass Electrofishing Predicts Trout Abundance In Mountain Streams With Sparse Habitat. *N. Am. J. Fish. Manage.* 18: 940–946.
- L'Abée-Lund J.H., Vøllestad L.A. & Beldring S. 2004. Spatial and temporal variation in the grilse proportion of Atlantic salmon in Norwegian rivers. *Trans. Am. Fish. Soc.* 133: 743–761.
- Lancaster J. & Belyea R. 2006. Defining the limits to local density: alternative view of abundance-environment relationships. *Freshwat. Biol.* 51: 783–796.
- Lapointe M. 2012. River geomorphology and salmonid habitat: Some examples illustrating their complex association, from redd to riverscape scales. In: Church M., Biron P.M. & Roy A.G. (eds.) *Gravel-bed rivers: Processes, tools, environments*. John Wiley & Sons, Chichester, pp. 193–215.
- Lindeman A.A., Grant J.W.A. & Desjardins C.M. 2014. Density-dependent territory size and individual growth rate in juvenile Atlantic salmon (*Salmo salar*). *Ecol. Freshw. Fish* DOI: 10.1111/eff.12120.
- Linnansaari T., Keskinen A., Romakkaniemi A., Erkinaro J. & Orell P. 2010. Deep habitats are important for juvenile Atlantic salmon *Salmo salar* L. in large rivers. *Ecol. Freshw. Fish* 19: 618–626.
- Milner N.J., Wyatt R.J., & Scott M.D. 1993. Variability in the distribution and abundance of stream salmonids, and the associated use of habitat models. *J. Fish Biol.* 43: 103–119.
- Moir H.J., Soulsby C. & Youngson A.F. 1998. Hydraulic and sedimentary characteristics of habitat utilized by Atlantic salmon for spawning in the Girnock Burn, Scotland. *Fish. Manag. Ecol.* 5: 241–254.
- Moir H.J., Gibbins C.N., Soulsby C. & Webb J.H. 2004. Linking channel geomorphic characteristics to spatial patterns of spawning activity and discharge use by Atlantic salmon (*Salmo salar* L.). *Geomorphology* 60: 21–35.
- Morantz D.L., Sweeney R.K., Shirvell C.S. & Longard D.A. 1987. Selection of microhabitat in summer by juvenile Atlantic salmon (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* 44: 120–129.

- Mäki-Petäys A., Muotka T. & Huusko A. 1999. Densities of juvenile brown trout, *Salmo trutta*, in two subarctic rivers: assessing the predictive capability of habitat preference indices. *Can. J. Fish. Aquat. Sci.* 56: 1420–1427.
- Mäki-Petäys A., Huusko A., Erkinaro J. & Muotka T. 2002. Transferability of habitat suitability criteria of juvenile Atlantic salmon (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* 59: 218–228.
- Mäki-Petäys A., Erkinaro J., Niemelä E., Huusko A. & Muotka T. 2004. Spatial distribution of juvenile Atlantic salmon (*Salmo salar*) in a subarctic river: size-specific changes in a strongly seasonal environment. *Can. J. Fish. Aquat. Sci.* 61: 2329–2338.
- Niemelä E., Mäkinen T.S., Moen K., Hassinen E., Erkinaro J., Länsman M. & Julkunen M. 2000. Age, sex ratio and timing of the catch of kelts and ascending Atlantic salmon in the subarctic River Tenö. *J. Fish Biol.* 56: 974–985.
- Nislow K.H., Armstrong J.D. & Grant J.W.A. 2011. The role of competition in the ecology of juvenile Atlantic salmon. In: Aas Q, Einum S., Klemetsen A., Skurdal S. (eds.), *Atlantic salmon Ecology*. Blackwell Publishing Ltd, Oxford, pp. 171–197.
- Nislow K.H., Einum S. & Folt C.L. 2004. Testing predictions of the critical period for survival concept using experiments with stocked Atlantic salmon. *J. Fish Biol.* 65 (Suppl. A): 188–200.
- Nislow K.H., Folt C.L. & Parrish D.L. 1999. Favorable foraging locations for young Atlantic salmon: applications to habitat and population restoration. *Ecol. Appl.* 9: 1085–1099.
- Nislow K.H., Folt C.L. & Parrish D.L. 2000. Spatially explicit bioenergetic analysis of habitat quality for age-0 Atlantic salmon. *Trans. Am. Fish. Soc.* 129: 1067–1081.
- Nislow K.H., Folt C.L. & Seandel M. 1998. Food and foraging behaviour in relation to microhabitat use and survival of age-0 Atlantic salmon. *Can. J. Fish. Aquat. Sci.* 55: 116–127.
- Nordwall F., Näslund I. & Degerman E. 2001. Intercohort competition effects on survival, movement, and growth of brown trout (*Salmo trutta*) in Swedish streams. *Can. J. Fish. Aquat. Sci.* 58: 2298–2308.
- O'Connor K.I., Metcalfe N.B. & Taylor A.C. 2000. The effects of prior residence on the behaviour and growth rates of juvenile Atlantic salmon (*Salmo salar*). *Behav. Ecol.* 11: 13–18.
- Orell P. & Erkinaro J. 2007. Snorkelling as a method for assessing spawning stock of Atlantic salmon, *Salmo salar*. *Fish. Manag. Ecol.* 14: 199–208.
- Quinn G.P. & Keough M.J. 2002. *Experimental design and data analysis for biologists*. University Press, Cambridge.
- Railsback S.F., Stauffer H.B. & Harvey B.C. 2003. What Can Habitat Preference Models Tell Us? Tests Using a Virtual Trout Population. *Ecol. Appl.* 13: 1580–1594.
- Rosenfeld J. 2003. Assessing the Habitat Requirements of Stream Fishes: An Overview and Evaluation of Different Approaches. *Trans. Am. Fish. Soc.* 132: 953–968.
- Roy M.L., Roy A.G., Grant J.W.A. & Bergeron N.E. 2013. Individual variability of wild juvenile Atlantic salmon activity patterns: effect of flow stage, temperature, and habitat use. *Can. J. Fish. Aquat. Sci.* 70: 1082–1091.
- Scruton D.A. & Gibson R.J. 1993. The development of habitat suitability curves for juvenile Atlantic salmon (*Salmo salar*) in riverine habitat in insular Newfoundland, Canada. *Can. Spec. Publ. Fish. Aquat. Sci.* 118: 149–161.
- Skoglund H. & Barlaup B.T. 2006. Feeding pattern and diet of first feeding brown trout fry under natural conditions. *J. Fish Biol.* 68: 507–521.
- Snyder D.E. 2003. *Electrofishing and its harmful effects on fish*. Information and Technology Report USGS/BRD/ITR--2003-0002: U.S. Government Printing Office, Denver, CO.

- Steingrimsson S.O. & Grant J.W.A. 1999. Allometry of territory size and metabolic rate as predictors of self-thinning in young-of-the-year Atlantic salmon. *J. Anim. Ecol.* 68: 17–26.
- Steingrimsson S.O. & Grant J.W.A. 2003. Patterns and correlates of movement and site fidelity in individually tagged young-of-the-year Atlantic salmon (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* 60: 193–202.
- Symons P.E.K. 1971. Behavioural adjustment of population density to available food by juvenile Atlantic salmon. *J. Anim. Ecol.* 40: 569–587.
- Taggart J.B., McLaren I.S., Hay D.W., Webb J.H. & Youngson A.F. 2001. Spawning success in Atlantic salmon (*Salmo salar* L.): a long-term DNA profiling-based study conducted in a natural stream. *Mol. Ecol.* 10: 1047–1060.
- Teichert M.A.K., Foldvik A., Forseth T., Ugedal O., Einum S., Finstad A.G., Hedger R.D. & Bellier E. 2011. Effects of spawning distribution on juvenile Atlantic salmon density and growth. *Can. J. Fish. Aquat. Sci.* 68: 43–50.
- Terrell J.W., Cade B.S., Jeannette C. & Thompson J.M. 1996. Modeling stream fish habitat limitations from wedge-shaped patterns of variation in standing stock. *Trans. Am. Fish. Soc.* 125: 104–117.
- Thomson J.R., Weiblen G., Thomson B.A., Alfaro S. & Legendre P. 1996. Untangling multiple factors in spatial distributions: lilies, gophers, and rocks. *Ecology* 77: 628–642.
- Torgersen C.E., Baxter C.V., Ebersole J.L. & Greswell R.E. 2012. Incorporating spatial context into the analysis of salmonid–habitat relations. In: Church M., Biron P.M. & Roy A.G. (eds.), *Gravel-bed rivers: Processes, tools, environments*. John Wiley & Sons, Chichester, pp. 216–224.
- Ugedal O. & Finstad A.G. 2011. Landscape and land use effects on Atlantic salmon. In: Aas Q, Einum S., Klemetsen A. & Skurdal S. (eds.), *Atlantic Salmon Ecology*. Blackwell Publishing Ltd, Oxford, pp. 333–349.
- Van Horne B. 1983. Density as misleading indicator of habitat quality. *J. Wildlife Manage.* 47: 893–901.
- Vehanen T. 2003. Adaptive flexibility in the behavior of juvenile Atlantic salmon: short-term responses to food availability and threat from predation. *J. Fish Biol.* 63: 1034–1045.
- Vehanen T., Mäki-Petäys A., Aspi J. & Muotka T. 1999. Intercohort competition causes spatial segregation in brown trout in artificial streams. *J. Fish Biol.* 55: 35–46.
- Venter O., Grant J.W.A., Noel M.V. & Kim J.-W. 2008. Mechanisms underlying increase in young-of-the-year Atlantic salmon density with habitat complexity. *Can. J. Fish. Aquat. Sci.* 65: 1956–1964.
- Webb J.H., Fryer R.J., Taggart J.B., Thompson C.E. & Youngson A.F. 2001. Dispersion of Atlantic salmon (*Salmo salar*) fry from competing families as revealed by DNA profiling. *Can. J. Fish. Aquat. Sci.* 58: 2386–2395.
- Wootton R.J. 1999. *Ecology of teleost fishes*. 2nd ed. Chapman & Hall, London.
- Økland F., Thorstad E.B. & Naesje T.F. 2004. Is Atlantic salmon production limited by number of territories? *J. Fish Biol.* 65: 1047–1055.