

HABITAT REQUIREMENTS OF JUVENILE SALMONIDS

Towards ecologically-based fisheries management in boreal
streams

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MÄKI-PETÄYS**

Department of Biology

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Abstract

For effective management of stream salmonids, it is essential to (i) assess the productive potential of a stream in relation to species-specific habitat requirements, and to (ii) identify the key factors underlying any bottleneck periods during the life cycle of a fish. For this purpose, this PhD-thesis focuses on the mechanisms of habitat selection by juvenile salmonids in boreal streams.

Habitat preference curves for depth, water velocity, substrate and instream cover for brown trout (*Salmo trutta L.*) in river Kuusinkijoki, northeastern Finland, indicated that larger trout preferred deeper stream areas than age-0 trout did. In summer, all size-classes of trout preferred small substrates, whereas in winter, areas with cobble-boulder substrates were preferred. Winter presents a bottleneck period for trout in boreal streams; therefore winter habitat curves should be incorporated into habitat-hydraulic models when estimating habitat suitable for riverine trout in areas with severe winter conditions. The preference curves of age-0 trout were validated by correlating age-0 trout density with habitat availability at multiple sites in two boreal rivers where trout densities were monitored in 1988-1995. Substrate preference curve was effective in predicting trout densities among sites, whereas among-year variation in trout densities was best predicted by depth-related preference curves.

The responses of age-0 brown trout and grayling (*Thymallus thymallus L.*) to enhancement structures were investigated in artificial stream flumes. For both species a crucial habitat factor was the availability of flow refuges, especially in winter. In another experiment, age-1 trout dominated over age-0 trout when competing for velocity and overhead cover they both found suitable, emphasizing the role of intraspecific interactions in habitat selection by trout. These results suggest that the provision of a broad diversity of microhabitats should be a major goal in rehabilitation programs for fishery purposes.

A new method, combining GIS-assisted (Geographical Information System) approach with geostatistical tools, facilitated the detection of fish distribution patterns in a spatially heterogeneous stream habitat. The method will likely prove valuable when determining appropriate sampling scale(s) for future studies of fish habitat selection in relation to benthic prey. Unlike Arctic bullhead (*Cottus poecilopus*, Heckel), trout did not show any aggregation with their benthic prey according to spatially-referenced data on the distribution of lotic fishes and benthic macroinvertebrates within a stream reach.

Keywords: brown trout, habitat selection, stream rehabilitation, winter.

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List of original papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals:

- I Mäki-Petäys A, Muotka T, Huusko A, Tikkanen P & Kreivi P (1997) Seasonal changes in habitat use and preferences by juvenile brown trout, *Salmo trutta*, in a northern boreal river. *Can J Fish Aquat Sci* 54: 520-530.
- II Mäki-Petäys A, Muotka T & Huusko A. Densities of juvenile brown trout, *Salmo trutta*, in two subarctic rivers: assessing the predictive capability of habitat preference indices. *Can J Fish Aquat Sci*, in press.
- III Mäki-Petäys A, Vehanen T & Muotka T. Microhabitat use by age-0 brown trout and grayling: seasonal responses to streambed manipulation under fluctuating flow. Manuscript, submitted.
- IV Vehanen T, Mäki-Petäys A, Aspi J & Muotka T. Intercohort competition causes spatial segregation in brown trout in artificial streams. *J Fish Biol*, in press.
- V Muotka T, Mäki-Petäys A, Kreivi P & Högmander H (1998) Spatial associations between lotic fish, macroinvertebrate prey and the stream habitat: a multi-scale approach. *Boreal Env Res* 3: 371-380.

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1. Introduction

During the last two decades it has become obvious that the study of running waters cannot be carried out by excluding the role of human activities, nor is it possible to ignore the urgent need for conservation (Allan 1995). At the same time, stream ecology has taken long steps from a descriptive to a more theoretically-oriented science (Muotka 1994). Describing repeated patterns of stream organisms, populations and communities in relation to their biotic and abiotic environments is a prerequisite for testing general ecological theories in stream communities. This may in turn provide mechanistic explanations for anthropogenic changes in stream and river ecosystems. Such information is especially important, if the changes are general and controlled by few key factors, and if these factors can be affected by management (e.g. Fausch *et al.* 1988). Therefore it is evident that we need to increase our knowledge about the potentially complex habitat requirements of stream-dwelling organisms to facilitate mitigating the negative effects of human impacts on the stream environment.

Many salmonid fish species are born in running waters and, after smoltification, they migrate to a lake or sea to grow, returning to their natal river to spawn. Some salmonids or stocks of them, however, reside in streams all of their life (Wootton 1990). In contrast to the classical view of salmonid parr as site-specific stream dwellers (for reviews, see Gowan *et al.* 1994, Fausch & Young 1995), recent observations of stream salmonids have also documented extensive habitat shifts from their nursery areas to varying parts of a watercourse (estuaries, tributaries, lakes), depending on environmental conditions (e.g. Erkinaro 1997). Unfortunately, damming rivers for hydropower purposes and dredging them for log floating, have affected the juvenile lifestages of stream salmonids negatively. Management plans to restore impacted rivers should provide spawning environments, as well as suitable rearing habitats for juvenile salmonids to re-establish the threatened or extinct salmonid populations in streams (Heggenes 1989; see also Fausch & Young 1995, Erkinaro & Gibson 1997).

Many fish enhancement projects have focused on improving the stream habitat for salmonids by increasing the streambed complexity, and thereby providing more instream cover for salmonids (e.g. Moore & Gregory 1988, Binns 1994, Gowan & Fausch 1996, Sundbaum & Näslund 1998). Extensive projects have also been launched in Finland to restore rivers formerly dredged and channelized for log transport. The goal of these

projects is to create a more heterogenous stream habitat, aiming at the well-being of salmonid fishes and their food organisms (Laasonen *et al.* 1998, Yrjänä 1998). Habitat-hydraulic models are commonly used to estimate the quantity of habitat suitable for salmonids at different stream flows (e.g. Heggenes 1996), and they may also be used as an evaluation tool for different enhancement projects (e.g. Shuler & Nehring 1994). This thesis is a part of an ongoing project established to assess, by the means of habitat-hydraulic modelling, how successful these rehabilitation programs have been in satisfying the habitat requirements of juvenile salmonids (see Huusko & Yrjänä 1997).

Stream salmonids undergo marked seasonal (e.g. Cunjak & Power 1986, Heggenes *et al.* 1993) and ontogenetic (Bohlin 1977, Moyle & Baltz 1985, Greenberg *et al.* 1996) habitat shifts; therefore the season- and size (age)- specific knowledge of their habitat requirements is essential for adequate modelling. To study these questions both field and laboratory approaches were adopted in this thesis. First, I developed season-specific (summer, autumn, winter) preference curves for depth, mean water velocity, substrate size and cover of aquatic vegetation for three size-classes of juvenile brown trout (*Salmo trutta* L.) in a northern Finnish river (I) to facilitate regionally relevant application of habitat-hydraulic models in Finland (see Huusko & Yrjänä 1997). Then I evaluated the accuracy of these preference curves in predicting the densities of age-0 trout in two subarctic rivers (II). In artificial stream channels, I examined the microscale behavioural responses of age-0 brown trout and grayling (*Thymallus thymallus* (L.)) to streambed complexity under varying flows (III).

Habitat-hydraulic models have at times met with limited success, probably because spatially and temporally varying biological factors have not been incorporated into the models (e.g. Orth 1987), and because the models may operate at a larger spatial scale than that relevant to fish (e.g. Heggenes 1996). It is obvious that more information about these issues with respect to the habitat selection of fish, is required for biologically more realistic habitat models. Accordingly, the purpose of paper IV was to study whether intercohort competition may cause spatial segregation among size-classes of juvenile trout, and whether this segregation is seasonally variable. Finally, because the appropriate scale for a study is often difficult to determine *a priori* (e.g. Muotka & Penttinen 1994), a multi-scale approach was adopted (V) to examine the spatial association between juvenile brown trout, Arctic bullhead (*Cottus poecilopus*, Heckel), macroinvertebrate prey and the stream habitat.

2. Material and methods

2.1. Study area

The field work was conducted in rivers Kuusinkijoki (I, II and V) and Kitkajoki (II). These rivers are 3rd-order tributaries to the river Oulankajoki, near the Arctic Circle in northeastern Finland (a detailed map appears in paper II). Both rivers flow through spruce and pine forests and discharge into Lake Paanajärvi, and finally to the White Sea in Russia. The water quality of river Kuusinkijoki is slightly degraded by human activities, whereas river Kitkajoki is in a near pristine condition (Koutaniemi & Kuusela 1993). Water temperature peaks at about 17-19°C in late July to early August and falls below 1°C in late October. Both rivers are mainly ice-covered from mid-November to late April. The hydrology of the study rivers is characterized by a high spring flood in May and a smaller flood in late September - early October. Compared to the flow regime of River Kuusinkijoki (mean: 10 m³/s, range: 1-60 m³/s), River Kitkajoki is less variable (mean: 21 m³/s, range: 8-50 m³/s). Brown trout and Arctic bullhead are the dominant fish species in both rivers, although other species, especially European grayling and European minnow (*Phoxinus phoxinus* (L.)), also occur in these rivers.

2.2. Laboratory streams

The experimental studies were performed using hatchery reared salmonids in three (IV) or four (III) identical indoor flumes located at the Finnish Game and Fisheries Research Institute, Kainuu Fisheries Research and Aquaculture, northern Finland. The flumes were 6 m long and 37 cm wide, with a maximum depth of 30 cm. Water from the hatchery main storage was transferred by two submersible pumps into two large containers (2000 l each), and both containers supplied water into two of the flumes. Fish were always allowed to acclimate 48 h before they were used in the trials, to allow them to recover from the handling stress and transportation. Artificial light was provided on a 12:12 light:dark photoperiod (room light, 125 lx: red light 3 lx). Three (IV) or four (III) video

cameras per flume connected to video monitors facilitated observation of fish from an adjacent room. Observations were made either only in daytime (III), or during both day and night (IV). Both experiments were conducted in summer and winter.

2.3. Seasonal and ontogenetic changes in habitat preference of trout (I)

Juvenile brown trout were located by means of underwater observation or modified point electrofishing procedure (e.g. Moyle & Baltz 1985) and divided into three size-classes (4-9, 10-15, 16-22 cm). Habitat characteristics were measured from each fish location in six separate stream sections (range of areas: 600-3000 m²), and to quantify habitat availability, the same variables were measured from the same sampling sections using a stratified random sampling protocol. Season-specific preference curves were developed by relating use to habitat availability for four habitat variables: depth, mean water velocity, dominant substrate size and cover of aquatic vegetation. A two-way ANOVA was conducted to test for potential season x size-class interaction effects in trout habitat use. In addition, discriminant function analysis (DFA) was employed to examine the multivariate nature of seasonal variation in habitat availability and habitat use by trout. Principal component analysis (PCA) was used to examine whether habitat use differed between trout size-classes, and whether trout habitats constituted a nonrandom subset of the habitat available in the study reach.

2.4. Predictive capability of habitat preference indices (II)

Fourteen to 25 stream sites (mean area \pm 1 SE: 97 \pm 3.1 m²) were electrofished during eight summers using the three-pass removal method, and fish densities were calculated according to Bohlin *et al.* (1989) to obtain estimates of late summer densities of age-0 brown trout. Habitat characteristics (depth [d], dominant substrate size [s], surface water velocity [v]) were quantified at each site immediately after electrofishing. Trout densities at each study site were correlated with site-specific suitability values, ranging from 0.0 (unsuitable) to 1.0 (optimal). These suitability values were obtained by converting the mean value of the measured habitat variables at each sampling site to preference indices based on the corresponding preference curves for age-0 trout in summer (P[d], P[v], P[s]). Densities were also correlated with calculated composite preference indices P[dv], P[ds], P[dsv] (see Gan & McMahon 1990). To assess the importance of substrate for trout during their first year of life, a ratio called 'apparent survival' (the density of age-1 trout at a site in year *t* vs the density of age-0 trout at the same site in year *t*-1, see Gowan & Fausch 1996) was correlated with summer and winter indices of substrate preference for age-0 trout and with the same index for age-1 trout in summer.

2.5. Microscale behavioural responses of salmonids to stream enhancement structures (III)

Microhabitat selection by age-0 brown trout and grayling was investigated in experimental flumes with either 'channelized' or 'restored' streambed structures. Fish were exposed to low- and high-flow treatments in both summer and winter. Water velocities used by fish, Donnelly's (1978) index of aggregation, and the distances from each fish position to the (i) nearest stone and (ii) the inlet of the flume, represented dependent variables in the study. The experimental design incorporated 8 treatment combinations in a 2 x 2 x 2 factorial structure. Because the same fish were observed during both low- and high-flow treatments, flow was a within-subject factor in repeated measures ANOVA, whereas season and flume type represented between-subject factors. Species- and season-specific preference curves for bottom water velocities were developed in both flume types by relating velocities used by fish to those available in the flumes.

2.6. Intercohort competition of juvenile brown trout (IV)

The role of intercohort competition in causing spatial segregation between age-0 and age-1 brown trout was examined in artificial flumes during two seasons (winter vs summer) and at different times of day (day vs night). Competition treatments were: (1) two small trout, (2) two small and two large trout, and (3) two large trout per stream channel. The channels were longitudinally divided into three experimental units (1 m each), each of which consisted of two velocity shelters on the opposite sides of the stream, one of the shelters providing overhead cover for the fish. Time of day was a within-subjects factor, whereas season and treatment were between-subject factors, when differences in swimming movements, aggressions and velocity use by trout were analysed using repeated measures ANOVA. Differences in shelter use by trout size-classes were tested by logit analysis (Christensen 1990), where the proportion of a habitat type (velocity shelter, shelter with cover, open stream) used was the response variable, and treatment, season, time of day and fish size (small vs large) were the explanatory variables.

2.7. Spatial scales of lotic fish and their habitat (V)

A multiscale approach was adopted to study the spatial association between stream fish, their food resources and habitat characteristics. The sampling area of 23 m x 4.5 m was divided into 279 grid cells, each 0.75 m x 0.5 m. The abundance of brown trout and Arctic bullhead were quantified within each cell by the means of point electrofishing (see paper I), and habitat variables (depth, water velocity, substrate size and instream vegetation) were also measured from each cell. Benthic samples were collected from paving bricks (14 cm x 13 cm) in the centre of every other cell. The spatial patterns of habitat variables and invertebrate abundances were visualized by coloured contour plots, and fish

distributions were superimposed on these plots. Two geostatistical methods, semivariogram and kriging (see Rossi *et al.* 1992), were also used to study the spatial patterns among the data.

3. Results and discussion

3.1. Habitat requirements of juvenile trout (I)

Larger trout generally preferred deeper stream areas than young-of-the-year fish (I, see also paper V). When observed over seasons, the optimal ranges for depth were 5-35, 40-60, and 50-75 cm for 4-9, 10-15, and 16-22 cm trout, respectively (I). This bigger fish - deeper habitat pattern has been documented in numerous studies of habitat selection by stream fish (e.g. Bohlin 1977, Power 1987, Harvey & Stewart 1991). In late summer and autumn age-0 trout favoured stream areas with large amounts of aquatic vegetation. The largest trout (16-22 cm) occupied habitats with little vegetation cover throughout the year, and in winter, all trout avoided areas with a high percentage of aquatic vegetation. At the onset of winter, all trout size-classes moved into shallower water, but this mainly reflected seasonal variation in habitat availability. Cunjak and Power (1987) and Heggenes *et al.* (1993) suggested that instead of depth, velocity refuges and overhead cover are probably the primary factors in winter habitat selection of trout. In winter, trout preferred slowly flowing stream areas, whereas in other seasons the mean water velocities used by trout paralleled habitat availability. In summer, all size-classes of trout preferred small substrate sizes, whereas in winter, areas with cobble-boulder substrate sizes were preferred, especially by trout larger than 10 cm. Due to the reduced swimming ability of fish at low water temperatures (e.g. Rimmer *et al.* 1985, Graham *et al.* 1996), the interstitial spaces of coarse substrates may be the prime determinant of the suitability of a stream area as wintering grounds for salmonid fish (Rimmer *et al.* 1984, Heggenes *et al.* 1993).

Discriminant analysis ranked water velocity and depth as the most important variables in differentiating among habitats used by trout at different seasons. Similar rankings of physical habitat variables in trout microhabitat use have been reported by Gatz *et al.* (1987) and Heggenes and Saltveit (1990). When observed across seasons, principal component analysis revealed the clearest pattern of nonrandom habitat use for the smallest size-class of trout. The microniches of these fish were characterized by slower water velocities, lower depths, smaller substrates and a higher amount of aquatic vegetation than generally available in the stream habitat. A tendency of larger trout (>10 cm) to

occupy stream areas with cobble and boulder substrates and low amounts of instream vegetation distinguished their habitat use from the available habitat and from the habitat use by the smallest trout (I).

3.2. Trout densities in relation to habitat preference indices (II)

Different habitat preference curves were effective in predicting late summer densities of age-0 brown trout in among-site vs among-year comparisons. Substrate suitability index based on the summer preference curve correlated with the among-site variation of trout densities most significantly, explaining 21-74 % of this variation within the study years. The trout density among years (pooled over sampling sites) correlated, however, positively and most significantly with depth-related preference indices; preference for depth (P[d]) and the composite indices P[ds] and P[dsv] were best able to predict the negative effect of high discharge on trout abundance. Similarly, Nehring and Anderson (1993) found significant negative correlations between discharge and densities of brown and rainbow trout (*Oncorhynchus mykiss*) in their 13-year study in 11 Colorado streams. These results suggest that extreme flow events during the early life stages may have far-reaching effects on trout population dynamics (see also Shuler & Nehring 1994).

Habitat models can be expected to correlate closely with fish abundance only if a species' tolerable range for a habitat variable is exceeded (Shirvell 1989). This may explain why trout densities in this study were not related to the availability of suitable depths at the study sites: at most sites (ca. 80 %) P[d] obtained values near the optimum range (0.8 - 1.0) for trout fry, which probably prevented the detection of any real associations between P[d] and trout density. However, the negligible relationship between P[v] and trout density does not indicate that water velocity is not an important determinant of trout distribution at a smaller scale than used in this study (3 measurements / site). Stream salmonids are known to prefer low-velocity positions adjacent to swift currents to minimize their energy expenditure, yet to have access to invertebrate drift (Fausch 1984, Hughes & Dill 1990, Hill & Grossman 1993). Thus, it is obvious that the sampling resolution for water velocity used in this study was not appropriate for describing microhabitat availability for trout (see also Heggenes 1996).

The strongest dependence of stream salmonids on suitably sized substrate particles is usually found during winter (e.g. Rimmer *et al.* 1984, Näslund 1989, Heggenes *et al.* 1993, see also paper I). In study II, sites with abundant fry in late summer often rated poorly as winter substrates. In addition, sites with the highest apparent survival obtained low indices when summer substrate curves for age-0 trout were used. These results suggest that at the onset of winter, most fry abandoned their summer habitats and moved to adjacent wintering areas where coarser substrates were available. This hypothesis is supported by many authors, who have documented considerable distances (200 m or more) moved by juvenile trout in search of suitable overwintering habitats (Cunjak & Power 1986; Chisholm *et al.* 1987).

3.3. Microhabitat selection by trout and grayling in relation to streambed complexity and flow variation (III)

The observed differences in microhabitat selection by age-0 brown trout and grayling under similar experimental conditions support Greenberg *et al.*'s (1996) contention that differences between these two species in microhabitat use result from selective rather than interactive segregation. A majority of trout preferred low-velocity refuges (see also Heggenes & Traaen 1988), whereas grayling were mostly found in swifter currents. Juvenile brown trout mostly occupied positions with a snout water velocity less than 20 cm/s (as reviewed by Heggenes 1989). Such low velocities are also used by the smallest fry of grayling, but less frequently when their length exceeds 6 cm (Sempeksi & Gaudin 1995). However, since both trout and grayling selected lower velocities in winter than in summer, the potential for interspecific competition may increase with decreasing water temperature.

A homogenous substrate and a high streamflow increased the downstream movement of trout in both summer and winter. Grayling, however, were similarly affected by these factors only in winter. Larger grayling (>6 cm) are able to use much higher water velocities than their smaller conspecifics (Sempeksi & Gaudin 1995, see also Valentin *et al.* 1994); i.e. neither substrate complexity nor flow level induced downstream movement of grayling (mean length 7.6 cm) in our summer experiments. While the increased downstream movement of salmonid fry under high streamflows has been repeatedly documented (e.g. Ottaway & Forrest 1983, Irvine 1986, Crisp & Hurley 1991a, b), the role of substrate complexity has been rarely addressed (but see Meyer & Griffith 1997). However, irrespective of substrate complexity, the tendency for downstream movement was higher in winter for both species, which is well in accordance with Heggenes and Traaen's (1988) finding that salmonid fry are able to withstand higher velocities at higher water temperatures.

The availability of flow refuges was much more restricted in channelized than restored flumes, and this translated to narrower preference curves with lower optimum values in channelized flumes especially for trout. Restricted availability also produced a highly clumped distribution pattern for trout in channelized flumes, especially in winter, also resulting in increased downstream movement of trout fry in winter. Overall, the observed linkage between velocity preferences and downstream movement of salmonid fry is an intraspecific analogue to the general ecological phenomenon that narrow-niched species may be more controlled by the abiotic environment than broad-niched species.

3.4. Intercohort competition of juvenile brown trout (IV)

Behavioural shifts in both age-0 and age-1 brown trout in the presence of the other size-class were observed in experimental flumes. Larger trout increased their activity and behaved more aggressively when together with smaller trout, whereas small trout moved less and were rarely aggressive in the presence of larger trout. These results are consistent with Bohlin's (1977) field observations that age-1 trout dominate over age-0 trout

when competing for territories they both find suitable. In Greenberg *et al.*'s (1996) experiments, the habitat selection by small (ca. 10 cm) trout was not affected by the presence of larger trout (ca. 12 cm).

Size-dependent habitat use is probably a trade off between predation risk, feeding opportunities and social interactions (Hughes 1998). Daytime foraging by trout in summer would involve an increased risk of predation from visually hunting predators, especially for larger trout, possibly producing the "bigger fish-deeper habitat relationship" (see e.g. Schlosser 1987, Godin 1997, papers I and V). In winter, trout are primarily nocturnal, and selecting deep water would probably incur little, if any, benefits as regards to predator avoidance then. Nevertheless, by providing shelter from stream current, depth may still contribute importantly to habitat selection by trout even in winter (Heggenes *et al* 1993).

Fish behaviour changed also seasonally, trout of both size classes being less mobile and preferring lower water velocities in winter than in summer. Both size classes increased their use of instream cover in winter. Such wintertime aggregation of trout to low-velocity habitats is well documented in previous studies (e.g. Cunjak & Power 1986, Heggenes & Saltveit 1990, see also papers I and III). When both size classes were present, only small trout changed their use of water velocities and cover, whereas large trout did not. The results indicate that intercohort competition may indeed cause spatial segregation among size groups of brown trout.

Contrary to some recent findings reporting diel variation in the behaviour of salmonid fish (e.g. Valdimarsson *et al.* 1997, Metcalfe *et al.* 1998), no diel periodicity was observed in the behaviour or microhabitat use of brown trout regardless of season. Heggenes *et al.* (1993) found brown trout to be nocturnally active at low water temperatures during winter, whereas in daytime trout were concealed within the interstitial spaces of the stream substrates. The lack of diel periodicity may be due to the use of hatchery fish in this experiment; hatchery fish are reported to be day-active irrespective of water temperature (Pirhonen 1998). Furthermore, nocturnal behaviour of salmonids is at least partly a means of avoiding diurnal predators (Valdimarsson & Metcalfe 1998), which hatchery fish are unfamiliar with.

3.5. Spatial relations between lotic fish, benthic prey and the stream habitat (V)

Overlay maps obtained from field mapping surveys show the tendency of large trout (10-15 cm) to occupy deeper stream areas with coarser substrates than the ones typically used by smaller trout (5-10 cm). Spatial relations between fish and their prey was detected for only Arctic bullhead. Large bullhead (> 4 cm) aggregated in areas providing the highest abundance of benthos, especially semisessile invertebrates (larval stages of black flies and filter-feeding caddisflies). For predominantly drift-feeding trout (Allan 1981, Grant & Noakes 1986, McIntosh & Townsend 1995), benthic samples may give a somewhat biased view of prey availability. However, if spatial associations exist, they should be

found between fish and semisessile prey (see Sih 1984), because mobile prey types may continuously shift their distribution in relation to local predation pressure (Tikkanen *et al.* 1994, Forrester 1995).

High-density patches of trout and bullhead were in separate sections of the sample reach. The spatial interactions between these two species appear to be highly scale-dependent: inhibition at small scales (intraspecific aggregations) vs coherence at larger scales (whole stream sections; A. Mäki-Petäys, unpubl.) Thus, the near-absence of trout from high density prey patches may be explained by interference between trout and bullhead. In many occasions bullhead are suggested to compete for food with juvenile salmonids (e.g. Andreasson 1971, Mason & Machidori 1976, Andersson *et al.* 1986). In addition, Gaudin and Caillere (1990) suggested that juvenile brown trout avoid areas with high density of bullhead (*Cottus gobio* L.).

Semivariograms showed spatial dependence in the data for water depth and density of semisessile invertebrates, especially at lags shorter than 2 metres. There was probably, however, also some dependence in invertebrate densities at scales below the smallest sampling distance (1.0 m). It is impossible to sample fish and benthic macroinvertebrates with the same accuracy using the same sampling grid. Thus, while the measurements of this study were accurate for fish distributions, a denser grid should have been used for benthic invertebrates. Overall, the GIS-assisted (Geographical Information System) approach described in this study combined with standard geostatistical tools and statistical modelling may prove valuable for determining appropriate sampling scales for future studies of fish habitat in relation to the distribution of benthic and drifting prey (see also Muotka & Penttinen 1994).

4. Implications for ecologically-based fisheries management in boreal streams

It is not surprising that habitat-hydraulic modelling has won increasing popularity among fisheries biologists when selecting management strategies for stream salmonids. By estimating the amount of habitat suitable for fish in different phases of their life span, such modelling facilitates evaluation of the potential of a stream reach for fish production. Recently, however, many authors have underlined the flexibility and dynamic nature of fish habitat use, and habitat suitability criteria and modelling based on single snapshot studies have met with limited success (e.g. Orth 1987, Heggenes 1996). Since seasonal and ontogenetic changes in habitat use and preference by juvenile salmonids were evident in all studies included in this thesis, I suggest that the minimum requirement for increasing the biological realism of instream models is that the size structure of the fish population under study and the seasonality of resource availability and use be incorporated into the models.

Stream habitat and fish abundance will be tightly linked only if habitat availability is the prime determinant of fish density (e.g. Milner *et al.* 1985). Many other factors (see paper I) can contribute in determining fish abundance, potentially masking any habitat-fish density relationships (Milner *et al.* 1985, Orth 1987, Heggenes 1996). As with any model, the predictive accuracy and realism of the physical habitat model output is limited by the user's understanding of the underlying assumptions and limitations inherent in the model, in addition to the biological knowledge and expertise incorporated into the modelling and decision-making process (Huusko & Yrjänä 1997; see also Gan & McMahon 1990, Heggenes 1996). Unfortunately, the construction of independent habitat preference criteria for all of the various aspects of fish habitat use will not be logistically feasible. However, when interpreting the output of habitat-hydraulic models in relation to fish abundance, we should at the very least be able to estimate the extent to which biotic interactions and other factors, not included in the model, may modify fish habitat selection. The correlative nature of most field studies may, however, prevent insight into the actual mechanisms underlying the responses of fish populations to variations in stream habitat conditions. Consequently, it is advisable to test the detected patterns by manipulative experiments under controlled conditions (III, IV; see also Fausch 1992). Furthermore, a higher sampling resolution and a multi-scale sampling design may provide us with a bet-

ter understanding of the mechanistic links between fish distribution and the spatial heterogeneity of the stream habitat. Finally, because experimental studies in indoor flumes mainly focus on small scale behavioural responses of young fish, inevitably under artificial conditions, a larger scale experimental system consisting of replicable seminatural stream units is urgently needed to facilitate habitat studies at scales relevant to all size groups of fish.

Assessing the productive potential of a stream in relation to species-specific habitat requirements and identifying key factors underlying 'bottleneck' periods for fish populations are the cornerstones for effective management of threatened salmonid populations (see Fausch *et al.* 1988, Thorfve & Carlstein 1998). In boreal areas, harsh winter conditions are critical for salmonid production (II and III), and as pointed out by Cunjak (1996), it is "...not until we consider winter as part of the field season rather than a time to work up summer data, will we be able to effectively conserve and manage fish habitat." Wintering trout often shelter among the interstitial spaces of coarse substrates (e.g. Heggenes *et al.* 1993), and to facilitate the survival of juvenile trout through winter, stream management programs need to ensure that such spaces are abundantly available in trout wintering areas, and that seasonal habitat shifts between summer nursery areas and overwintering habitats are unrestricted (see Cunjak 1996). Therefore, winter preference curves should be used when habitat-hydraulic modelling is applied in areas where winter conditions may limit habitat availability for juvenile trout.

Habitat preference curves developed for brown trout in this thesis, combined with habitat-hydraulic modelling, should facilitate the estimation of habitat suitability for juvenile trout during different phases of their life in boreal streams. This will help us elaborate stream restoration schemes that take the habitat requirements of juvenile trout into serious consideration. Then, management efforts could be focused on preventing stream habitat deterioration, such as loss of trout nursery areas, instead of merely compensating losses in trout production by stocking. This approach, i.e. assessment of the amount of habitat suitable for trout in a stream, should also be helpful when determining appropriate stocking densities for different streams. From the management point of view, it is important to notice that microhabitats selected by trout fry differed from those selected by grayling. Both these species are important game fish and often live sympatrically in many northern streams. If the goal of a rehabilitation program is to provide suitable living conditions for both trout and grayling, species-specific preference curves should be used in habitat-hydraulic modelling. Since such detailed knowledge is often lacking, however, the most prudent option may often be simply to provide a broad diversity of microhabitats to ensure suitable living conditions for various life-stages of most stream salmonids (see also Greenberg *et al.* 1996, Huusko & Yrjänä 1997). A heterogenous stream habitat is a worthy goal also because it provides scope for seasonal and ontogenetic variation in microhabitat selection by both trout and grayling.

5. References

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