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Mari Nykänen

Habitat Selection by Riverine Grayling, Thymallus thymallus L.

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UNIVERSITY OF JYVÄSKYLÄ

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To the most beautiful of all angels,
my grandmother, Rauha Unelma

ABSTRACT

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The aim of this thesis was to examine the habitat selection by riverine European grayling (*Thymallus thymallus* L.) in different life stages and seasons. Habitat preferences and movement patterns of grayling are still poorly known, and new information is needed to better protect and manage the species and its critical habitats. Spawning habitat preference data were collected in the River Kuusinkijoki, northern Finland. This information was combined with data from the literature to develop generalized suitability criteria that could be potentially applicable to a wide range of rivers. It was found that locations with swift water velocities and gravel-pebble substrata were consistently used by grayling to bury their eggs. In contrast, use of water depth varied between sites. Significant size-related changes were found in the feeding habitat requirements of larval grayling in the River Kuusinkijoki. The smallest larvae had the strictest habitat requirements, especially regarding water velocity. As the fish grew larger, they gradually shifted into deeper and faster habitats with coarser substrata and less vegetation. A transferability test was carried out on the River Kuusinkijoki criteria for the first feeding habitat of larval grayling, and on a corresponding criteria set obtained from literature for a French river. The results suggested that universal criteria for water velocity may exist for larval grayling, and that these criteria may suffice when predicting habitat suitability to larval grayling by habitat-hydraulic modelling in rivers. Radiotelemetry studies on adult grayling in rivers Kuusinkijoki and Kemijoki revealed significant seasonal changes in the fish habitat selection. In summer and spring, the fish preferred shallower and faster flowing habitats with coarser substrata than in autumn and winter. In autumn, grayling moved mostly downstream from riffle reaches to overwinter in slowly flowing river areas. In spring, at the time of ice break-up, the fish moved mostly upstream to potential spawning sites in riffles and runs. Some fish remained within the spawning reaches during summer, whereas others shifted to new swiftly flowing areas. Within seasons, the fish movements were mainly local. The present findings suggest that availability of suitable habitats for egg burial, for newly hatched larvae, and for overwintering may be especially critical to grayling populations, whereas the summer habitat use of adults is more flexible.

Key words: Grayling; habitat preference; habitat shifts; larvae; overwintering; Salmonidae; seasonal movements; spawning; telemetry.

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LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following original papers, which will be referred to in the text by Roman numerals (I-VI).

I Nykänen, M. & Huusko, A. 2002. Suitability criteria for spawning habitat of riverine European grayling. ***Journal of Fish Biology 60: 1351-1354***.

II Nykänen, M. & Huusko, A. 2003. Size-related changes in habitat selection by larval grayling (*Thymallus thymallus* L.). ***Ecology of Freshwater Fish 12: 127-133***.

III Nykänen, M. & Huusko, A. 2004. Transferability of habitat preference criteria for larval European grayling (*Thymallus thymallus* L.). ***Canadian Journal of Fisheries and Aquatic Sciences 61: 185-192.***

IV Nykänen, M., Huusko, A. & Mäki-Petäys, A. 2001. Seasonal changes in the habitat use and movements of adult European grayling in a large subarctic river. ***Journal of Fish Biology 58: 506-519***.

V Nykänen, M., Huusko, A. & Lahti, M. 2004. Changes in movement, range and habitat preferences of adult grayling from late summer to early winter. ***Journal of Fish Biology 64: 1386-1398.***

VI Nykänen, M., Huusko, A. & Lahti, M. 2004. Spring migration of grayling from an overwintering pool to spawning and feeding areas: seasonal ranges, activity and habitat preferences. Manuscript.

RESPONSIBILITIES OF MARI NYKÄNEN IN THE ARTICLES OF THIS THESIS

Paper I. I was mostly responsible for the study plan. Ari Huusko and I together carried out the field work. I analysed the data and wrote the article.

Paper II. I planned the study together with Ari Huusko. We and a field crew carried out the field work. I analyzed the data and wrote the article.

Paper III. I planned the study and carried out the field work together with Ari Huusko. I was responsible for data analysis, except for the Surfer-maps that were produced by Ari Huusko, and I wrote the article.

Paper IV. I planned the study together with Ari Huusko based on his preliminary ideas. I carried out the field work together with a field crew. I did all the data analyses except for the DFA-analysis and the construction of the suitability curves which were done jointly with Aki Mäki-Petäys. I wrote the paper except for the part of methods dealing with DFA and suitability functions which was written jointly with Mäki-Petäys.

Paper V. I planned the study based on Ari Huusko's preliminary ideas. I was responsible for the initiation of the field work, later continued by a field crew. Ari Huusko and I together designed the data collection for hydraulic modelling, and Markku Lahti constructed the hydraulic model. I analyzed the data and wrote the paper, except for the parts dealing with modelling for which Lahti and Huusko were mainly responsible.

Paper VI. I planned the study together with Ari Huusko based on my preliminary ideas. We carried out the field work together with a field crew. Ari Huusko and I together designed the data collection for hydraulic modelling and Markku Lahti constructed the hydraulic model. I analyzed the data and wrote the paper, except for the parts dealing with modelling for which Lahti and Huusko were mainly responsible.

Jyväskylä January 19th, 2004 Mari Nykänen

1 INTRODUCTION

'Habitat' is the place or area where an organism lives, an area of the physical environment distinct from other areas in a range of abiotic and biotic characteristics (Rabeni & Sowa 1996, Kramer et al. 1997). In riverine environments, the most important habitat characteristics affecting distributions and abundances of fishes are availability of food, water temperature, water quality, flow regime, presence of competitors and predators, and physical habitat structure (Orth 1987, Kramer et al. 1997).

In streams, habitat variables operate at different spatial scales from ecoregion or stream basin level (macrohabitat), to pool-riffle reach level (mesohabitat), and to the exact fish position level (microhabitat) (Bovee 1982, Stalnaker et al. 1995, Rabeni & Sowa 1996, Parasiewicz & Dunbar 2001). At the scale of macrohabitats, variables such as water temperature or water quality can determine the general suitability of an area to a species and thus fish presence or absence (Bovee 1982, Stalnaker et al. 1995, Crisp 1996, Rabeni & Sowa 1996). At local scales (meso- and microhabitats), characteristics of the physical habitat are often considered the most important factors determining fish distributions. For salmonids, these factors are water depth, velocity, substratum type, and cover (e.g. Heggenes 1988, Stalnaker et al. 1995, Knapp & Haiganoush 1999).

Fish habitat selection is dynamic and it can vary with habitat availability (Heggenes 1991, 1996, Garner 1997), presence of predators (Schlosser 1988, Eklöv et al. 1994, Brown 2003) and competitors (Greenberg 1999) or density of conspecifics (Hughes 1992, Bult et al. 1999, Armstrong & Griffiths 2001). Fish often also have different habitat requirements depending on their size (Sagnes et al. 1997, Bremset & Berg 1999, Heggenes et al. 2002, Rosenberger & Angermeier 2003), activity (Shirvell & Dungey 1983), time of day (Baxter & McPhail 1997, Roussel & Bardonnet 1999) or season (Brown & Mackay 1995, Kristiansen & Døving 1996, Mäki-Petäys et al. 1997, Heggenes & Dokk 2001). Temporal and ontogenetic changes in habitat use can occur over scales ranging from a meter or less (e.g. shifts between shallow-water habitats used at night and deeper water used during daytime; Sempeski & Gaudin 1995a, Roussel & Bardonnet 1999) to hundreds of kilometres (e.g. the macrohabitat shifts made by anadromous salmonids as they move between the sea and the river). At all times, however, fish select positions to maximize their fitness within the limits of their competitive abilities and available habitat conditions. Habitat selection is a trade-off between growth (food intake, energy used for swimming, etc.), reproductive success, and survival, which includes predator avoidance and protection from adverse physicochemical conditions (Fausch 1984, Hughes & Dill 1990, Cunjak 1996, Kramer et al. 1997).

Knowledge about fish habitat selection helps to understand the functioning of riverine ecosystems. It is also crucial for solving various problems related to stream management, exploitation and enhancement of fish stocks or conservation of endangered species. For example, examination of fish movement patterns can help differentiate between separate populations, and thus determine appropriate units for conservation and fisheries management (Fausch & Young 1995, Kristiansen & Døving 1996). Data on the timing and patterns of fish movements are needed also to estimate the sizes of mobile populations, to design correctly timed and targeted fishing restrictions, and to locate any possible obstacles to natural migration behaviour (Hellawell 1976, Linløkken 1993, Kramer et al. 1997). Data on fish habitat requirements are important in the planning of where, when, and at which densities to stock fish in order to strengthen natural populations (Aprahamian et al. 2003). Moreover, habitat enhancements aimed at increasing the production of fish stocks cannot be effectively planned without knowing the habitat requirements of the target species (Reeves et al. 1991, Rabeni & Sowa 1996, Kramer et al. 1997, Hendry et al. 2003). Particularly important is to recognize the so called 'habitat bottlenecks', i.e. essential habitat types associated with certain life stages or seasons that are in short supply and thus limit the population sizes (Orth 1987, Bovee et al. 1998).

For the purposes of stream management, it is often necessary to develop quantitative indices or criteria that describe habitat suitability to fish. Habitat-hydraulic modelling, for example, is a widely used management tool where fish habitat criteria are combined with hydraulic models to estimate flow-related changes in the quantity and quality of available microhabitats or to evaluate the effects of habitat enhancement actions (Bovee 1986, Stalnaker et al. 1995, Huusko & Yrjänä 1997, Gibbins & Acornley 2000, Parasiewicz & Dunbar 2001). Several modelling frameworks are now available but the original physical habitat simulation model (PHABSIM) and its modifications are still the ones most widely used (Stalnaker et al. 1995, Parasiewicz & Dunbar, 2001). For these models, habitat suitability criteria can be expressed in a variety of types and formats, some of the most common ones being binary criteria (e.g., unsuitable vs. suitable water depth), univariate habitat utilization curves (based on frequency of use; e.g., the most often used depth is considered optimal) and habitat preference curves or other preference indexes where habitat use is related to habitat availability (Jacobs 1974, Bovee 1982, 1986, Parasiewicz & Dunbar 2001).

Validity of habitat hydraulic modelling, as well as other management actions, depends on how accurately the chosen criteria describe and predict the habitat requirements of the target species (Bovee et al. 1998). Habitat preference criteria are usually considered more representative than utilization functions, but both criteria types are somewhat sensitive to habitat availability at the criteria development site (Bovee 1986, Heggenes 1988, Heggenes et al. 1996). It is also important to develop criteria using fish observation methods – such as snorkeling, visual observation, electrofishing or telemetry – relevant to the study site, species, and life stage to avoid observation bias (Bovee 1986, Heggenes et al. 1990, Thorfve 2000). Criteria used as a basis for management actions should be carefully stratified to represent all the essential life stages of a species. For salmonids, separate criteria at least for the spawning habitat, the summertime feeding habitat, and the overwintering habitat appear to be necessary (Heggenes 1988, Northcote 1995, Crisp 1996). Stratification of criteria by fish size is most important for the first year or two of fish life when habitat requirements change more frequently than in the adulthood (Bovee 1986).

Because habitat selection is such a multi-faceted issue, possibly affected by local species composition and prevailing environmental conditions, it has been recommended that site-specific suitability criteria should be used as a basis for management actions (Orth 1987, Heggenes 1996). This is not always feasible, however. For example, if a study river differs significantly from its natural state, as rivers needing management often do, fish numbers or habitats available in it may be too few for a reliable determination of habitat preferences. The ultimate goal would be to recognize universal patterns in fish habitat selection, i.e. criteria applicable to a variety of rivers (Bovee 1986, Bovee et al. 1998). This can be done by testing the transferability of existing criteria across sites. So far, only a few validation tests have been carried out (Beecher et al. 1993, Thomas & Bovee 1993, Boudreau et al. 1996, Freeman et al. 1997, Guay et al. 2000, Mäki-Petäys et al. 2002).

Habitat selection criteria of most stream fishes are still poorly known, including the European grayling (*Thymallus thymallus* L.). Grayling is currently vulnerable in several parts of its distribution area, mainly due to changes in the physical habitat, pollution, and overfishing (Seppovaara 1982, Sjöberg & Henricson 1985, Magee 1993, Northcote 1995, Persat 1996, Ibbotson et al. 2001, Uiblein et al. 2001). Grayling is a medium-sized salmonid (maximum length about 50-60 cm; Seppovaara 1982, Nordwall et al. 2002) present in an area extending up to the Great Britain in the west, the Pyrenees and northern Italy in the south, parts of Norway and majority of Finland and Sweden in the north, and the Ural Mountains in the east. The species occurs mainly in rivers but also in lakes and in brackish water along the coasts of Finland and Sweden in the Bothnian Bay (Ehnholm 1937, Müller & Karlsson 1983, Northcote 1995). Grayling is often present in the same clean, oxygen-rich waters as brown trout (*Salmo trutta*) and Atlantic salmon (*S. salar*) (e.g. Crisp 1996, Degerman & Sers 1992, Degerman et al. 2000), and like them, it is a popular game fish. Unlike salmon and trout which spawn in autumn (Armstrong et al. 2003), grayling spawn in March-June at water temperatures 4-7°C (up to 15°C), soon after ice break-up (Northcote 1995). It is known that riverine grayling spawn in relatively shallow water with gravelly substrata and swift velocities (Fabricius

& Gustafson 1955, Müller 1961, Gönczi 1989, Persat & Zakharia 1992, Sempeski & Gaudin 1995b, Poncin 1996, Darchambeau & Poncin 1997). Larvae hatch three-four weeks after the spawning at 15-20 mm length, with yolk sack still present (Penáz 1975, Scott 1985). The first feeding habitats of larvae are usually near the river margins in relatively shallow and slowly flowing water, where the fish mostly occupy the upper parts of the water column (Scott 1985, Bardonnet et al. 1991, Sempeski & Gaudin 1995c). During the first month after emergence the larvae gradually shift into deeper and faster water (Bardonnet et al. 1991, Sempeski & Gaudin 1995a). According to Sagnes et al. (1997), the shift coincides with morphological 'jumps' which increase the hydrodynamic potential of the fish.

Once grayling have metamorphosed into the juvenile form (fish lengths >35 mm), they are mostly found close to, or within, the main channel. During the night most young-of-the-year grayling move closer to the shore to rest (Penáz 1975, Scott 1985, Bardonnet et al. 1991, Sempeski & Gaudin 1995a). In summer, subadult and adult riverine grayling tend to reside in riffle areas with relatively swift velocities and coarse substrata, although they do occur in slowly flowing river stretches (Peterson 1968, Dyk 1984, Greenberg et al. 1996, Prenda et al. 1997, Mallet et al. 2000). Adult grayling have been observed to migrate in autumn to overwinter in relatively deep and slowly flowing river stretches or lakes (Andersen 1968, Zakharchenko 1973). In spring they migrate to their spawning sites and thereafter to the feeding sites (Andersen 1968, Witkowski & Kowalewski 1988, Linløkken 1993, Parkinson et al. 1999, Meyer 2001). Most information on the seasonal movement patterns and microhabitat use of grayling is, however, qualitative or based on small sample sizes. Data on the autumn and winter habitat selection of grayling are virtually lacking. Therefore, new studies quantifying the habitat selection of grayling are urgently needed in order to better protect and enhance the grayling populations and their habitats.

The objective of this thesis was to collect data applicable for stream management on the movements and physical habitat selection of riverine grayling. The study covers several of the critical phases in a salmonid's life and extends over four seasons. In paper I, the spawning habitat preferences of grayling were examined in a boreal river. These data were then combined with information available in literature to develop generalized habitat suitability curves which could be potentially applicable to a wide variety of rivers. In paper II, habitat preference criteria stratified by fish size were developed for larval grayling, and in paper III, the transferability of these criteria, as well as those developed for larval grayling by Sempeski & Gaudin (1995d), were tested across sites. In papers IV, V and VI, the movement patterns, habitat use, and habitat preferences of adult grayling were examined in different seasons, including summer, autumn, early and late winter, and the spawning period in spring.

2 MATERIALS AND METHODS

2.1 Study area

Habitat selection of grayling was studied in three boreal rivers located close to the Arctic circle in northern Finland. Studies I, II, V and VI were conducted in the River Kuusinkijoki, study III was conducted both in the River Kuusinkijoki and the River Maaninkajoki, and study IV was conducted in the River Kemijoki (Fig. 1).

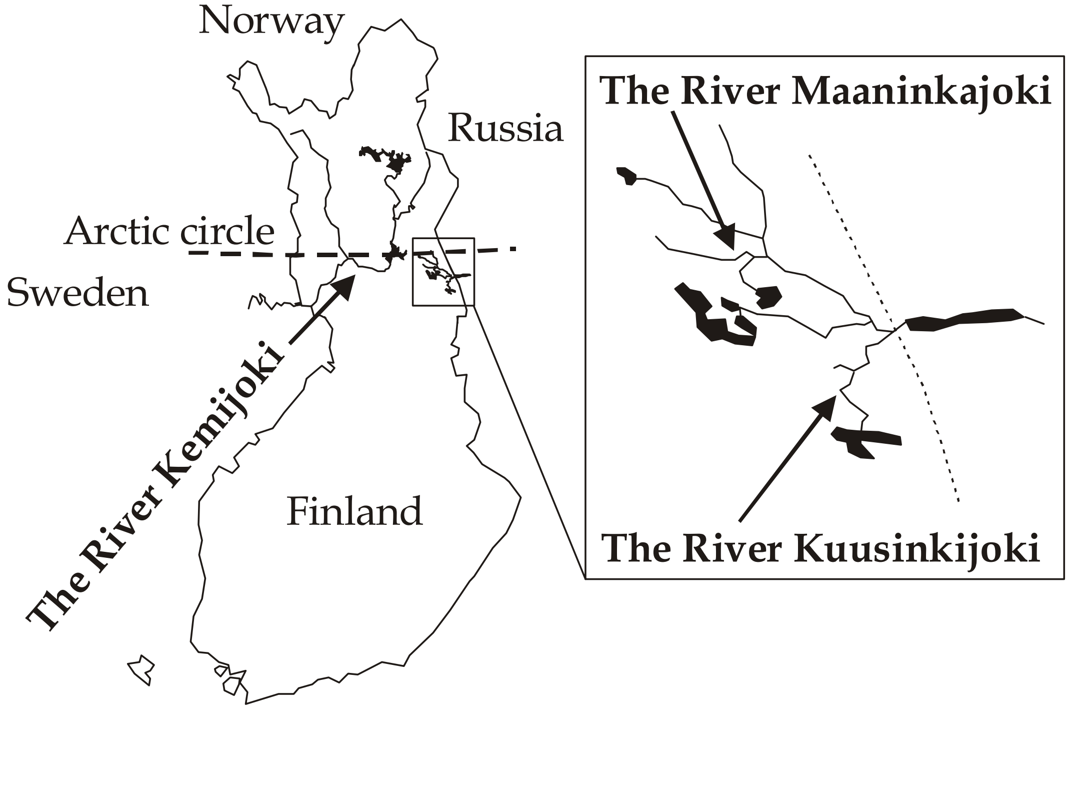

FIGURE 1 Location of the three study rivers. Arrows indicate the main study sites in the River Kuusinkijoki (studies I-III, V-VI), in the River Maaninkajoki (III), and in the River Kemijoki (IV).

The River Kuusinkijoki is a 20 km long tributary of the River Oulankajoki which discharges in the Lake Paanajärvi in Russia. The River Kuusinkijoki is dammed at its origin but the flow rate is maintained near natural with no diel regulation. The flow regime of the river (annual mean 10 $m^3 s^{-1}$) is typical of boreal streams, so that the minimum flows (down to 1 $m^3 s^{-1}$) occur in winter and peak flows (up to 60 $m^3 s^{-1}$) soon after the snowmelt in May-June. Most of the river is ice-covered from mid November to late April, and water temperature is usually highest (up to 18-20° C) in July. The channel form is near-natural except for a 1.8 km long man-made section in the upstream end of the river, below the hydropower plant. Fish species present are grayling, brown trout *Salmo trutta* L., minnow *Phoxinus phoxinus* (L.), whitefish *Coregonus lavaretus* (L.), northern pike *Esox lucius* L., alpine bullhead *Cottus poecilopus* Heckel, perch *Perca fluciatilis* L., ruffe *Gymnocephalus cernuus* (L.), roach *Rutilus rutilus* (L.), burbot *Lota lota* (L.), and nine-spined stickleback *Pungitius pungitius* (L.). Riparian community in the study site is dominated by coniferous trees (pine, spruce).

The River Maaninkajoki is also a tributary of the River Oulankajoki, but much smaller than the River Kuusinkijoki, with a discharge of 0.6 $m^3 s^{-1}$ during data collection in summer 2000. Fish species present in the River Maaninkajoki are the same as in the River Kuusinkijoki.

The River Kemijoki is a c. 600 km long regulated stream which flows through northern Finland and discharges into the Bothnian Bay with the mean annual rate of 550 $m^3 s^{-1}$ (range 100-4000 $m^3 s^{-1}$). There are seven hydropower plants in the main stem, and seven in the tributaries. Temperature and ice cover conditions are similar to those in the River Kuusinkijoki. There is strong diel variation in the water level at the site where study IV was conducted. Species present in the study area and maintained by regular stocking are whitefish, rainbow trout (*Oncorhynchus mykiss* (Walbaum)), brown trout, and grayling. Other species present include minnow, roach, perch, northern pike, burbot, Arctic char (*Salvelinus alpinus* (L.)) and bream (*Abramis brama* (L.)). The river flows mainly through pine-spruce forests.

2.2 Habitat suitability criteria for spawning sites (I)

In this study, the spawning habitat preference criteria of grayling were first determined in the River Kuusinkijoki in May 2001. Spawning sites were located by kick-sampling in four areas, and local water depths, mean velocities and dominant substratum sizes were determined both at the egg sites (habitat use) and along equally spaced transects in the studied areas (habitat availability). Habitat preferences for the measured variables were determined by Jacobs (1974) formula for resource selection. Secondly, generalized suitability curves were developed for the spawning habitat of grayling by combining the new data with data available in literature on the egg burial sites of grayling

(Fabricius & Gustafson 1955, Müller 1961, Gönczi 1989, Sempeski & Gaudin 1995b, Darchambeau & Poncin 1997). All information was converted to a comparable curve format (habitat utilization or habitat preference curves standardized to range from 0 to 1), and then averaged for each variable (depth, mean velocity and substratum) to produce the general models as described by Bovee (1986).

2.3 Size-related changes in habitat selection by larval grayling (II)

In this study, habitat selection by larval grayling was observed in daytime from soon after hatching until the end of the larval period (size range of the fish 13-35 mm) in June 2000. The larvae were located by eye and hand-netting in 5-m-long observation areas randomly distributed along stream margins (different areas sampled each day). A group of fish was the unit of observation, and habitat measurements were taken either at the position of individual fish or at the centre point of a shoal. Habitat availability was determined along transects. To determine the size-related changes in use and preference (electivity index D; Jacobs 1974) of depth, mean water velocity, dominant substratum size, and vegetation cover, the fish were divided into three size groups following the functional group classification suggested by Sempeski & Gaudin (1995a). According to these authors, fish of approximately 15-20 mm in length mainly occupy the dead zones near the river banks, and fish sizes 20-35 mm occupy areas close to the faster-flowing main channel. The shift between the two habitats occurs at the length of 20-25 mm and it is related to morphological changes that affect the fish hydrodynamics (Sagnes et al. 1997, Hedtke et al. 2001).

2.4 Transferability of preference criteria for larval habitat (III)

A modified suitability overlay test (Bovee 1986, Beecher et al. 1993, Guay et al. 2000) was used to test the transferability of two sets of habitat preference criteria for the first feeding habitat of larval grayling across sites. The first set of preference criteria (for depth, mean water velocity and dominant substratum) was obtained from Sempeski & Gaudin (1995c,d) in the format of preference curves ranging from 1.0 (optimal habitat) to 0.0 (unsuitable habitat). These criteria were based on data collected by visual sampling in the River Pollon, France, on <30 mm long fish (Sempeski & Gaudin 1995c). The second set of preference curves (depth, velocity, substratum, and vegetation cover) of similar format were developed from data collected in study II for larval grayling (<25 mm) in the River Kuusinkijoki, Finland. Transferability of both these criteria sets were tested to a site in the River Kuusinkijoki and a site in the River Maaninkajoki (target sites) in June 2001. The positions of larval grayling in these target sites were first mapped. Second, the suitability of the habitats available to the fish in these sites were evaluated with the preference criteria. Finally, the relationship between fish density and habitat quality was examined with rank correlation test. According to the suitability overlay test, criteria are transferable (valid) to a site if local fish densities increase with increasing suitability of habitat as predicted by the criteria (Bovee 1986). Univariate indices for depth, velocity, substratum and vegetation cover were tested singly and in various combinations (created by simple multiplication of indices; Bovee et al. 1998) to determine if some criteria or criteria combinations were potentially more useful than others in defining habitat suitability to larval grayling.

2.5 Seasonal movements and habitat use of adult grayling (IV-VI)

Seasonal movement patterns of adult grayling, as well as their habitat use and preferences, were examined in three studies and over four seasons: summer, the main growth period (e.g. Mallet et al. 1999); autumn and winter, the high-risk period with near-zero water temperatures and ice development (e.g. Cunjak 1996); spring, the time of reproduction (e.g. Northcote 1995). In the River Kemijoki (IV) and the River Kuusinkijoki (V-VI), altogether 64 fish were surgically tagged with internal radio-transmitters (weight in air 2.0-3.7 g; <2% of fish weight as recommended by Winter 1983) and subsequently monitored from a boat or the river bank once daily, mainly on weekdays (Mon-Fri). The grayling (Kemijoki: n = 30, mean ± s.d of total length: 32 ± 2 cm, weight 343 ± 48 g; Kuusinkijoki: n = 34, length 35 ± 2 cm, weight 403 ± 139 g) were captured on-site by angling (IV-V) or ice fishing (VI), and they were released to their capture areas shortly after they recovered from anaesthesia. Based on previous information on grayling development in the study region, the experimental fish were of age 4+-9+ and sexually mature (Myllylä 1982, Kännö & Salonen 1989, Huusko 1990).

In the River Kemijoki, two groups of fish were tagged to study the habitat selection by grayling in late summer (13 August - 13 September 1998; water temperature 12-16° C; 14 fish) and in autumn (2-30 October 1998; water temperature 1.7-6.7° C; 16 fish). In the River Kuusinkijoki, tags with longer battery life were used, and the behaviour of a group of 22 fish was monitored from late summer to early winter (16 August - 16 December 1999; water temperature 0-14.5° C), and the behaviour of a group of 12 fish from late winter to mid summer (12 April - 2 July 2001; water temperature 0-19° C). Daily fish locations were positioned on maps and the data were used to determine e.g. the net distances moved by the fish between consecutive days and the seasonal movement ranges. Habitat characteristics depth, mean velocity, and dominant substratum were measured at the fish sites from a boat in the River Kemijoki, and from a boat or by wading in the River Kuusinkijoki in 1999 (until the development of ice cover in mid November). In the River Kuusinkijoki in 2001, habitat characteristics at fish sites were determined by hydraulic modelling (ice-free period). For the River Kemijoki grayling, seasonal habitat utilization curves were developed, and for the River Kuusinkijoki grayling, habitat use within each season was compared to habitat availability (determined by hydraulic modelling within the stream reaches used by the fish in 1999 and 2001, respectively) to determine seasonal habitat preferences (electivity index D; Jacobs 1974).

3 RESULTS AND DISCUSSION

3.1 Spawning habitat requirements of grayling (I)

Based on the present and previous findings, the suitable ranges of mean velocity, dominant substratum size, and water depth for the spawning habitat of grayling are around 40-70 cm s^{-1}, 16-32 mm, and 10-110 cm, respectively. In the River Kuusinkijoki, used and preferred ranges of velocities and substrata (Table 1) were similar to those determined by Sempeski & Gaudin (1995b) for grayling in the River Pollon and the River Suran, France. In the French rivers, however, preference was for shallower water (10-30 cm) than in the Kuusinkijoki (>40 cm). When the results of these preference studies were contrasted with all other information on the spawning habitat of grayling (Fabricius & Gustafson 1955, Müller 1961, Gönczi 1989, Darchambeau & Poncin 1997), it appeared that regardless of geographical location (from France to northern Scandinavia) or stream size (from creeks to a large river), the substratum and current velocity requirements for egg burial are similar, whereas depth use varies more among sites. The relatively strict requirements for velocity and substratum size are understandable because: 1) females need to move the substratum to bury eggs, 2) the survival of eggs during incubation requires sufficient intragravel flow to bring oxygen and remove wastes, and 3) the fry need sufficiently loose substratum to emerge (Crisp 1996, Kondolf 2000). Influence of water depth on the spawning act or incubation success is less evident. So far, eggs of grayling have been found in relatively shallow water (5-106 cm; Fabricius & Gustafson 1955, I). Nevertheless, the methods used to locate spawning sites, i.e. visual observation and kick-sampling (Gönczi 1989, I), are restricted to relatively shallow areas or to areas with good visibility. Further studies using new methods are still needed to evaluate the suitability of water depths >1 m as spawning sites of grayling.

The generalized suitability criteria developed here should be evaluated on a case-by-case basis before use e.g. in habitat-hydraulic modelling (Bovee 1986). It is possible that the criteria for velocity, dominant substratum and depth at egg burial sites are not the only variables necessary to estimate the amount of suitable spawning habitat, i.e. the number of potential territories, in an area. Substratum characteristics other than dominant particle size, e.g. thickness of gravel bed or embeddedness, are potentially important determinants of spawning success (Kondolf 2000). Moreover, the size of the spawning territories (<1-16 m^2) guarded by male grayling depends on presence of visual cover. Cover is needed also by females who avoid aggressive contacts with males by remaining in nearby shelters until they are ready to spawn (Fabricius & Gustafson 1955). Finally, pools are needed as resting habitat by both sexes (Fabricius & Gustafson 1955, Sempeski & Gaudin 1995b).

TABLE 1 Values of water depth, mean velocity, dominant substratum type, and instream vegetation cover measured at sites used by grayling in the rivers Kuusinkijoki and Kemijoki: a) mean ± s.d. (for substratum the most often used size class); b) total range used; c) preferred range (determined as Jacobs D > 0.2 for this summary table; Jacobs 1974). See the original articles I-VI for numbers of measurements and methods used.

Life stage	Depth (cm)	Velocity (cm s^{-1})	Substratum particle size (mm)	Vegetation cover (%)
Egg burial sites (I)	a) 53 ± 13 b) 30-110 c) 40-60	a) 61 ± 16 b) 20-90 c) 40-70	a) 8-16 b) 2-64 c) 8-32	
Larvae (II): Small (central 50 %: 17-21 mm)	a) 27 ± 13 b) 10-60 c) 10-30	a) 5 ± 6 b) <40 c) <10	a) <0.07 b) <0.07-1024 c) <2	a) 32 ± 26 b) <90 c) 10-70
Middle-sized (22-25 mm)	a) 38 ± 19 b) <100 c) 30-90	a) 7 ± 8 b) <40 c) <10	a) 256-512 b) <0.07-1024 c) 0.07-2	a) 17 ± 21 b) <100 c) <40
Large (26-31 mm)	a) 55 ± 24 b) 10-110 c) 50-110	a) 14 ± 12 b) <50 c) 10-50	a) 256-512 b) 0.07-1024 c) 0.07-512	a) 12 ± 19 b) <80 c) <40
Adult summer (IV)	a) 240 ± 101 b) 50-550	a) 76 ± 34 b) 10-170	a) >256 b) >0.07	
Adult summer (V)	a) 98 ± 9 b) 40-140 c) 80-120	a) 48 ± 7 b) 10-100 c) 40-100	a) >256 b) >0.07 c) 2-64	
Adult summer (VI)	a) 143 ± 76 b) 10-300 c) 140-300	a) 51 ± 23 b) <100 c) 50-100	a) >256 b) <0.07- >256 c) 16-128	
Adult autumn (IV)*	a) 288 ± 100 b) 75-575	a) 54 ± 23 b) 20-100	a) 0.07-2 b) >0.07	
Adult autumn (V)*	a) 143 ± 22 b) 60-240 c) 100-240	a) 24 ± 8 b) <70 c) 10-30	a) 16-64 b) >0.07 c) 0.07-64	
Adult spawning season (VI)	a) 158 ± 84 b) 50-350 c) >60	a) 53 ± 24 b) <120 c) 40-70	a) >256 b) <0.07- >256 c) 0.07-128	

* Measured at similar flow level as the summer values in the same study.

3.2 Habitat requirements of larval grayling (II-III)

Within the first three weeks of their life, larval grayling in the River Kuusinkijoki gradually shifted from shallow slow-velocity habitats with fine substrata and abundant instream vegetation to deeper, more swiftly-flowing areas with coarse substrata and little vegetation (Table 1). Small and middle-sized larvae were significantly closer to shore (mean distance about 1 m) than the large larvae (2 m). These results support the idea of Sempeski & Gaudin (1995a), that larval grayling can be classified into functional size groups each using a different kind of habitat. Sagnes et al. (1997) related these habitat shifts to morphological changes during grayling ontogenesis. One significant change occurs at length 20-25 mm when the position of shoulder shifts posteriorly. This change makes the fish more streamlined and thus improves their swimming potential, making it possible for them to shift into faster water velocities (Sagnes et al. 1997). Indeed, the small and middle-sized larvae in the River Kuusinkijoki remained closer to shore and in slower water velocities than the large larvae (>25 mm). Habitat selection by the smallest larval group was most specialized with narrow ranges of water depth, velocity, and substratum. It is therefore likely that the availability of these habitats is particularly critical for the early survival of grayling.

Low mean water velocity appears to be an essential criterion for the first feeding habitat of larval grayling. The fish always select water velocities <20 cm s^{-1}. In contrast, use and preference of water depth or substratum size by the larvae varies somewhat between sites (Scott 1985, Bardonnet et al. 1991, Sempeski & Gaudin 1995a,c, study II). In study III, velocity preference criteria were the only habitat criteria that consistently transferred across river sites, i.e. fish density increased with habitat quality as determined by the velocity criteria (Spearman rank correlation coefficients ranging from 0.83 to 0.92). Univariate criteria for depth, substratum and vegetation cover, as well as their combinations, either failed to predict fish distributions or did so inconsistently. The usable range of water velocities for larval grayling is determined by their physical capabilities, which largely explains the universality of the velocity criteria. According to Scott (1985), grayling larvae of about 17 mm in length are able to sustain their position for 3 min in velocities near 14 cm s^{-1} (median result), and 25 mm larvae in 30 cm s^{-1}. In nature, the fish usually choose velocities about half of these values (Scott 1985).

Importance of water depth, cover, and substratum composition to larval grayling is less clear. The significance of these variables may vary between sites, depending on habitat availability or presence of predators. If both shallow and deep low-velocity sites are available, deep sites may be preferred by young grayling because of better access to food in them (Sempeski et al. 1998). Presence of predators may increase use of shallow water by young salmonids (Roussel & Bardonnet 1999). Often larval grayling are found in water depths <1 m, and they use relatively fine substrata. Both these characteristics are typical of slow-velocity marginal habitats. The fish do not seem to seek shelter within the substratum or vegetation, although they do use areas of slow velocities behind such objects (Scott 1985, Bardonnet et al. 1991, study II).

The present results (III) suggest that velocity criteria alone may be sufficient in habitat-hydraulic modelling when the goal is to estimate the amount of suitable habitat available to larval grayling. Inclusion of criteria that do not reliably describe the critical habitat characteristics of the fish may result in erroneous estimations of suitable habitat. It is, however, possible that yet untested factors such as the proximity of river bank or the location of the slow-velocity areas relative to faster water (which brings food to the fish), affect the value of otherwise suitable slow-velocity areas.

3.3 Seasonal changes in movements of adult grayling (IV-VI)

In the studies IV, V and VI, adult grayling were observed to be relatively localised within seasons, so that the mean seasonal home range size was <100 m in summer, autumn and winter, and <200 m during the spawning season. The mean net daily distance moved was 10-30 m in each season (Table 2, paper IV). The fish, however, moved distances up to 14 km (mainly 0.5-5 km) between the seasonal sites, mostly upstream in spring and downstream in autumn. The findings are in agreement with the previous observations on the mobility of grayling by Zakharchenko (1973) (capture-recapture data), Parkinson et al. (1999) (radiotelemetry on six fish) and Meyer (2001) (radiotelemetry on seven fish), who all observed seasonal fidelity to stream sections and moderate migration distances (0-37 km, mostly <1 km, to overwintering areas; 0-11 km, mostly <5 km, to spawning sites and further to summer feeding areas).

TABLE 2 Seasonal home range size of adult grayling in the River Kuusinkijoki (V-VI) and the net daily distance moved by fish. Values are mean ± s.d. (range).

Season	Home range length (m)	Daily net movement (m)*
Summer (V)	75 ± 146 (10-610)	18 ± 34 (0-144)
Summer (VI)	75 ± 54 (20-200)	11 ± 7 (3-26)
Autumn (V)	99 ± 46 (40-180)	15 ± 7 (6-36)
Winter (V)**	63 ± 69 (0-170)	19 ± 15 (0-33)
Winter (VI)	48 ± 21 (20-90)	13 ± 7 (6-30)
Spawning season (VI)	184 ± 239 (40-770)	29 ± 40 (7-139)

* Calculated as a mean of the mean values for individual fish.
**Pool sites to which the fish moved at temperatures near 0° C.

In late summer, grayling both in the River Kemijoki and in the River Kuusinkijoki mainly stayed within their capture riffles (IV, V). In autumn, however, the fish usually shifted (mostly within a week) to various slowly flowing river sections. In the River Kemijoki, the fish moved to the pool sites within the first half of October, at water temperature 2.0-6.5° C and during a variable but generally increasing trend in discharge due to autumn flood (IV).

In the River Kemijoki, the shift started in the end of August (14.5° C) and finished by the end of September (10° C), before the autumn flood. There are very few previous data on the timing of autumn migrations by grayling; according to Zakharchenko (1973), in the River Pechora, Russia, the movement occurs from September onwards. For large salmonids in general, a shift to deeper and more slowly flowing sites in autumn is commonly observed (e.g. Clapp et al. 1990, Brown & Mackay 1995, Cunjak 1996). The shift usually occurs before the development of ice cover, at water temperatures <10° C (Hillman et al. 1987, Jakober et al. 1998, Brown 1999). In summer, it is important for fish to obtain as much food as possible for growth and reproduction. In salmonids, this is often best achieved in relatively swift velocities where the encounter rate with drifting invertebrates is highest (Fausch 1984, Brittain & Eikeland 1988, Hughes & Dill 1990, O'Brien & Showalter 1993). As the water temperature drops in autumn, however, swimming ability of fish gradually decreases (Graham et al. 1996), as does also the density of drift (Brittain & Eikeland 1988). At some point, it is no longer profitable to remain in the energetically costly fast-velocity sites, and the fish shift into a strategy of conserving energy. This goal is best achieved by moving into lower water velocities (Cunjak 1996). It is unclear what exactly triggered the habitat shift in northern Finland, as the timing of the shift was very different in the two rivers despite similar water temperature and light conditions (IV, V).

Once water temperature dropped near 0° C in the beginning of November, several grayling in the River Kuusinkijoki abandoned their initial pool sites and moved to new slower flowing river stretches further downstream, joining some other tagged fish that had already arrived there in early autumn. The 'shifters' then stayed in these pools until the end of the monitoring in mid December 1999 when the slowly flowing river sections were already mostly covered by ice (V). No fish were monitored in mid winter, but it is possible that grayling used these pools throughout the cold season, because fish captured from under the ice in one of the overwintering pools of the River Kuusinkijoki in late winter 2001 (VI) stayed locally until the beginning of ice break up in the end of April. It is typical for salmonids to move little during winter. Nevertheless, occasional longer movements can occur if frazil and anchor ice accumulate permanently or temporarily in the sites preferred by fish (Brown & Mackay 1995, Komadina-Douthwright et al. 1997, Jacober et al. 1998, Brown 1999, Simpkins et al. 2000). Similar to the grayling in the River Kuusinkijoki (VI), bull (*Salvelinus confluentus*) and cutthroat trout (*Oncorhynchus clarki*) have been observed to shift between two pool sites as water temperature decreases near 0° C. According to the observers, the fish were excluded from their initial sites by underwater ice (Brown & Mackay 1995, Jacober at al. 1998). Development of ice may have been the reason also for the habitat shifts in the River Kuusinkijoki.

In spring, at the start of the ice break-up and spring flood (water temperature 0.3-3.7° C), the grayling in the River Kuusinkijoki (VI) left their overwintering sites and moved to potential spawning areas. One fish moved 7 km downstream, whereas others moved 0.1-6 km upstream. Although spawning could not be visually verified, sites suitable for egg burial were present in all areas chosen by the fish, and eggs were also found near several of the sites. At the end of the spawning season (estimated to end at 10° C in the River Kuusinkijoki, see methods in VI), approximately half of the tagged grayling moved into new sites 0.1-2.8 km up- or downstream for summer, whereas the others remained in the same sites as used during the spawning season. As in late summer, the fish remained most of the time locally also in early and mid summer. Nevertheless, as water temperature increased to 13.9-16.6° C in June, five fish made a 0.3-3.7-km-long shift from their first summer sites to new areas. None of the fish returned back to the (pool) sites used before the spawning migration as was observed by Parkinson et al. (1999) and Meyer (2001) in central Europe. It is likely that in the River Kuusinkijoki, suitable sites for spawning were available within areas suitable for feeding. It is unclear, however, what made half of the fish change their feeding ranges in mid summer. The increasing water temperature may have made the initially selected sites unprofitable, or the fish may have had to move because of an appearance of competitors or predators.

3.4 Seasonal changes in habitat use and preferences of adult grayling (IV-VI)

According to the present findings on the habitat use and preference of adult grayling in a large and a medium-sized boreal river, the fish select deeper sites with slower mean water velocity and finer substrata in autumn-winter than during spring (spawning season) and summer (Table 1, IV-VI). In summer, adult grayling in the River Kemijoki and in the River Kuusinkijoki mainly occupied sites with swift velocities, but the used mesohabitats ranged from riffles and runs to calmer river sections. This agrees with the observations of Peterson (1968), Dyk (1984), and Mallet et al. (2000). According to Mallet el al. (2000), adult grayling (length 28-44 cm) in the River Ain, France, prefer mean water velocities of 70-100 cm s^{-1} (used range approximately 20-130 cm s^{-1}). Similarly, velocities of 40-100 cm s^{-1} were preferred in the present studies (range 0-170 cm s^{-1}) (IV-VI). In contrast to these results, Greenberg et al. (1996) observed adult grayling (20-50 cm) in the River Vojmån, Sweden, to prefer velocities <10 cm s^{-1}. Use and preference of substrata has also varied between studies. In the River Ain, grayling used and preferred mainly gravelly substrata (availability of coarse substrata was low) (Mallet et al. 2000). By contrast, in the River Vojmån and in the present studies, grayling used (IV-VI) and preferred (Greenberg et al. 1996) coarser substrata. Range of water depths used by adult grayling in different rivers extends from <50 cm to >500 cm, but the fish prefer relatively deep water (mainly >1 m) (Greenberg et al. 1996, Mallet et al. 2000, Table 1, IV-VI). In the River Kuusinkijoki, the habitats used and preferred by adult grayling during the spawning season were very similar to the habitats occupied in summer. As an exception, the sites used during the spawning season contained more gravel substrata than the summer sites. In spring, the fish were observed during daytime. Therefore, the determined habitats may have contained positions used for spawning, resting (spawners sometimes enter their territories only in the afternoon; Fabricius & Gustafson 1955), and possibly also feeding.

The habitat characteristics of the autumn sites of adult grayling in the River Kemijoki and the River Kuusinkijoki were relatively consistent. In both rivers, the sites used in autumn were significantly deeper and slower than the summer sites, although the measured values in the much larger and deeper River Kemijoki were higher than in the River Kuusinkijoki in both seasons (Table 1). The most often used velocity range was <40 cm s^{-1} in both rivers in autumn. The fish were rarely observed in standing water. Instead, the fish appeared to select sites close to the main current in the slowly flowing river sections (IV-VI).

The relative importance of the physical habitat characteristics depth, velocity, and substratum type on fish habitat selection is difficult to determine because many habitat variables correlate with each other in nature. According to a discriminant function analysis, water velocity was the main factor differentiating the sites selected by adult grayling in summer and in autumn (IV). Importance of velocity is evident through its effect on the amount of prey the fish will encounter, and on the amount of energy the fish have to spend to maintain position (e.g. Hughes & Dill 1990). Apparently, depth is also important to adult grayling. Firstly, the fish clearly avoid shallow water (<50 cm) (Greenberg et al. 1996, Mallet et al. 2000, IV-VI) during both the warm and the cold seasons. The only exception being for the purpose of egg burial (I). Secondly, if only velocity were important to the fish, they would not have to move into sometimes remote deep pool sections in autumn to find suitable low-velocity microhabitats; slowly flowing water is generally available also within riffles (e.g. shallow river margins). Depth is potentially important to adult grayling because it can offer cover from avian predators or mammals during the ice-free period, and from ice during winter (e.g. Cunjak 1996). Depth also influences the number of prey a fish is able to detect and capture (Hughes & Dill 1990). Compared to velocity and depth, the significance of substrate composition to adult grayling is less clear. In the present studies, the fish clearly used coarser substrata during spring and summer (mainly boulders) than in autumn and winter (sand, gravel and pebbles) (IV-VI). Boulders were most common in the study rivers in fast-slowing sections and least common in pool sections. Therefore, substratum composition at the fish sites may have been merely a covariate of the water velocity and depth selected by the fish. Boulders can be important to brown trout as a form of cover (Heggenes 1988, 1996), but unlike trout, grayling occupy positions relatively far from instream cover (Greenberg et al. 1996).

4 CONCLUSIONS

The aim of this thesis was to strengthen our knowledge on the ecology of grayling by examining the habitat selection patterns of the species in the potentially critical periods of its life. These were the spawning season, the larval period, the feeding season, and the cold season with water temperatures close to 0° C. It was found that the microhabitat requirements of grayling for egg burial sites appear to be relatively universal, and the strictest criteria are perhaps for water velocity and dominant substratum size, whereas the use of water depth is more flexible. Significant size-related changes were observed in the habitat preferences of larval grayling within a period of only a few weeks. The smallest larvae had the strictest criteria, especially regarding low velocity and depth, whereas the largest larvae could already tolerate a much wider range of conditions, including velocities >20 cm s^{-1}. A transferability test on the microhabitat criteria for the first feeding habitat of larval grayling suggested that universal velocity criteria may exist for larval grayling, and that these criteria alone may be able to predict habitat suitability to the fish. Adult grayling in a large and a medium-sized river were observed to be very localised within each of the four seasons (movement ranges mostly <100 m), but to move longer distances between the seasonal habitats (up to 14 km). The habitat selection of adult grayling was found to change seasonally both at the mesohabitat and the microhabitat scale. During the spawning season and especially in summer, the fish occupied various swiftly flowing, yet relatively deep, riffles and runs. In autumn and winter, the fish were restricted to deep, slowly flowing pools.

Several possible management implications arise from the present findings, combined with previous information on grayling. Most evidently, a wide range of habitats are needed in a stream to maintain viable grayling populations. Since adult grayling are apparently able to move long distances, the sites can be also spatially separated. There must be no obstructions (such as dams), however, preventing fish movements. In regulated streams, it may be best to avoid large fluctuations in flow during the period of egg incubation and the first few weeks after the emergence of larvae. Sudden high flows, such as release of water from a hydro dam, could disturb the egg pockets or flush out the larvae from the shallows. In contrast, sudden low flows could leave the spawning redds without water or the larvae stranded (Peterson 1968, Crisp 1996, Kondolf 2000, Gaudin & Sempeski 2001). At the juvenile stage, grayling are already capable of adjusting their microhabitat selection according to changing flow levels (Valentin et al. 1994), and there is some indication that adult grayling remain within the same feeding areas even under fluctuating flows (Vehanen et al. 2003, study IV). In streams where physical habitat is limiting, grayling populations could be strengthened by increasing the amount of spawning habitats (in conditions of low siltation; Zeh & Dönni 1994). Logs or boulders could be added next to river banks so that new low-velocity zones suitable for larval grayling are created behind them. Overwintering habitat may become limiting to grayling stocks especially in areas where rivers are thickly covered by ice. If there are only a few overwintering pools available in a stream, it is possible that most adult fish are in those sites during the cold season. Hence, fishing restrictions may be necessary in the overwintering pools to avoid overfishing.

The habitat use and preference information provided in this thesis for the larval, spawning, and adult habitat can be used to develop habitat suitability indices applicable in the planning of habitat enhancement programs or regulation of river flows by habitat-hydraulic modelling. As suggested by Heggenes (1996), site-specific habitat criteria are probably always the best basis for management decisions. Nevertheless, it seems possible that transferable criteria could exist at least for periods when habitat use is limited by some inflexible physiological factors. Based on the present findings, habitat criteria for larval grayling (velocity use is limited by swimming ability) and egg incubation (survival is determined by e.g. supply of oxygen and stability of egg pockets) are potentially such universal criteria. Habitat selection by adult grayling is clearly more flexible, and transferable criteria may be more difficult to develop for them. The relative importance of habitat variables can vary between sites, and factors other than the physical habitat may be limiting to a fish population (Orth 1987, Heggenes 1996). Therefore, all habitat criteria, including those presented here, should be critically evaluated before use.

Much more research both in the field and in experimental conditions is still needed to get a more accurate picture on the habitat selection patterns of grayling. Interesting issues include the influence of biotic factors on the habitat selection of grayling, and the meaning of the spatial arrangement of different habitat types to the fish (Kocik & Ferreri 1998). Habitat selection by all size classes of grayling in winter should be further investigated. Little is known on the possible diurnal changes in the fish movements and habitat selection in different seasons. In addition, it would be worthwhile to monitor the behaviour of individual fish over several years to find out if grayling repeatedly return to the same overwintering, spawning and feeding sites (there is some indication of homing; Kristiansen & Døving 1996, Buzby & Deegan 2000, paper IV). Differences in habitat selection patterns of genetically divergent populations, like lacustrine, riverine, and sea-dwelling grayling, are mostly unknown.

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YHTEENVETO

Harjuksen (*Thymallus thymallus* L.) habitaatinvalinta virtavesissä

Tämän väitöskirjatyön tavoitteena oli tuottaa sekä ekologista perustietoa harjuksen habitaatinvalinnasta että sovellettavaa tietoa harjuskantojen hoidon perustaksi. Tutkimus koostuu kuudesta osatyöstä, joissa selvitettiin harjuksen kutuhabitaatin ominaisuuksia, vastakuoriutuneiden poikasten elinympäristövaatimuksia niiden ensimmäisten elinviikkojen aikana, aikuisten harjusten habitaatin valintaa eri vuodenaikoina ja aikuisten kalojen päivittäisiä liikkeitä kesällä, syksyllä, talvella sekä keväällä kutuaikana.

Lohikaloihin kuuluva harjus on viime vuosikymmeninä vähentynyt monin paikoin Euroopassa mm. saastumisen ja vesistörakentamisen vuoksi. Suomessakin vesiemme luonnontilaa muuttaneet toimet kuten uittoperkaukset, voimalaitokset patoineen ja säännöstelyineen, ojitukset sekä järvien lasku ovat heikentäneet tai jopa tuhonneet kantoja. Luonnontilansa menettäneiden jokien kunnostus on yleistynyt viimeisen vuosikymmenen aikana. Jotta kunnostuksilla olisi todellista merkitystä kalaston hyvinvoinnin kannalta, on työn pohjana oltava vankka ekologinen tietämys kohdelajien elintavoista sekä perusteista valita elinympäristönsä eli habitaattinsa. Jokiekosysteemeissä kalojen jakautumiseen ja runsauteen vaikuttavat mm. vedenlaatu, habitaatin fysikaalinen rakenne, virtaamaolosuhteet ja bioottiset tekijät, kuten ravintokohteiden esiintyminen, saalistajat ja kilpailu. Lisäksi kalojen habitaatinvalinta vaihtelee elämänvaiheiden ja vuodenaikojen mukaan. Samalla lajilla voi olla mm. erityinen kutu-, poikas-, ruokailu-, lepo- ja talvehtimishabitaatti. Yhdenkin habitaattityypin puute voi muodostua populaation hyvinvointia ja kokoa rajoittavaksi tekijäksi. Harjukselle räätälöityjen hoitotoimenpiteiden, kuten vesistökunnostusten, kalastuksen säätelyn ja istutusten, suunnittelua ja toteuttamista hidastaa ainakin osittain tiedon puute. Taimeneen ja loheen verrattuna harjuksen elinympäristövaatimuksia on tutkittu vähän. Vaikka harjuksen habitaatin käytöstä onkin olemassa jonkinlainen yleiskäsitys, on esimerkiksi kunnostusten apuna käytettävään elinympäristömallinnukseen saatavilla niukasti sovelluskelpoisia kvantitatiivisia tietoja.

Osatyössä I tarkasteltiin harjuksen kutuhabitaatin käyttöä ja preferenssiä (käytetty habitaatti suhteutettuna saatavilla olevaan habitaattiin) Kuusamon Kuusinkijoessa. Kutupesät paikannettiin etsimällä mätimunia potkuhaavimenetelmällä. Pesäpaikoista mitattiin veden syvyys, keskivirrannopeus ja pohjan raekoko (käyttö), ja samat muuttujat määritettiin myös säännöllisin välimatkoin valituista pisteistä koko tutkitulta alueelta (saatavillaolevuus). Harjukset suosivat kutupaikkoina alueita, joissa pohjan laatu oli pääasiassa soraa tai pikkukiviä (raekoko 8-32 mm) ja virtaus nopeahko (40-70 cm s^{-1}). Kutupesiä löydettiin veden syvyyksistä 40-110 cm, mutta käytetystä menetelmästä johtuen yli metrin syvyisiä alueita ei pystytty juurikaan tutkimaan, joten on mahdollista, että pesiä oli myös syvemmällä. Kirjallisuustietojen perusteella harjuksen kutuhabitaatin ominaisuudet ovat hyvin samanlaiset ympäri Eurooppaa, vaikka suurin osa tiedoista perustuukin vain kalan käyttämään habitaattiin ja harvoihin mittaustuloksiin. Muuttamalla kaikki saatavilla oleva tieto yhtäläiseen käyrämuotoon ja määrittämällä näistä keskiarvot laadittiin ehdotukset yleiskäyriksi, joiden avulla voi potentiaalisesti arvioida harjuksen kutuhabitaatiksi soveltuvan alueen määrää eri joissa. Yleiskriteerien mukaan optimaalisimmat ominaisuudet kutuhabitaatille ovat 16-32 mm raekoko, 50-60 cm s^{-1} virrannopeus ja 30-40 cm syvyys.

Osatyössä II tutkittiin harjuksen vastakuoriutuneiden poikasten habitaatinvalintaa ja siinä tapahtuvia muutoksia kalojen ensimmäisten elinviikkojen aikana (suomulliseen poikasvaiheeseen asti). Poikaset paikannettiin Kuusinkijoella visuaalisesti ja haavin avulla. Kalojen käyttämä ja suosima habitaatti erosi huomattavasti pienten, keskikokoisten ja suurten poikasten välillä siten, että koon kasvaessa kalat siirtyivät syvempään veteen isokivisemmille ja vähäkasvisemmille alueille. Pienet ja keskikokoiset poikaset suosivat hyvin hidasta virrannopeutta (<10 cm s^{-1}) ja olivat lähellä rantaviivaa (keskimäärin noin 1 m etäisyydellä), ja vasta suurimmat poikaset olivat selvästi kauempana rannasta (keskimäärin 1,9 m) ja nopeammassa virrassa (keskimäärin 14 cm s^{-1}). Tulos noudattaa ranskalaisten tutkijoiden teoriaa harjuksen poikasten asteittaisesta siirtymisestä joen rannoilta keskiuomaan ruumiin muotojen kehittyessä.

Osatyössä III testattiin saatavilla olevien preferenssikriteerien siirrettävyyttä eri jokialueiden välillä. Testattavat kriteerit olivat osatyössä II Kuusinkijoen pienimmille harjuksenpoikasille laaditut kriteerit ja kirjallisuudessa saatavilla olevat vastaavat kriteerit ranskalaisesta joesta. Niiden siirrettävyyttä testattiin Kuusinkijoessa ja läheisessä Maaninkajoessa. Kyseessä on ns. preferenssikriteerien validointitesti, jonka avulla voidaan selvittää ovatko jonkin lajin tai elinvaiheen preferenssikriteerit yleispäteviä vai vain paikallisesti sovellettavia. Samoin testin avulla voidaan arvioida, onko joku määritetyistä kriteereistä muita tärkeämpi tai yleistettävämpi kuin muut. Usein elinympäristömallinnuksessa suositellaan käytettäväksi paikan päällä määritettyjä habitaattikriteerejä. Tämä ei ole kuitenkaan aina mahdollista eikä edes järkevää (esim. kunnostuksen tarpeessa olevassa joessa kehitetyt kriteerit eivät välttämättä kuvaa kalojen todellisia preferenssejä), joten myös yleispätevien kriteerien määrittämiseen tulisi pyrkiä. Osatyön III tulosten perusteella vastakuoriutuneilla harjuksen poikasilla näyttäisi olevan yleispätevät valintakriteerit virrannopeudelle. Validointitesteissä virrannopeuskriteerit onnistuivat ennustamaan kalojen sijainnin koealueilla oikein, eli kalatiheys oli sitä suurempi mitä parempi oli habitaatin laatu virrannopeuden suhteen. Sen sijaan kriteerit syvyydelle, pohjan kivikoolle ja kasvillisuuspeittävyydelle, sekä erilaiset kriteerikombinaatiot, ennustivat kalojen sijoittumista koealueilla joko huonosti tai vaihtelevasti.

Osatöissä IV, V ja VI tarkasteltiin aikuisten (pituus >30 cm; yhteensä 64 kalaa) harjusten liikkeitä ja habitaatin valintaa telemetriaa apuna käyttäen Kemijoessa ja Kuusinkijoessa. Kaikissa tutkimuksissa kalat pyydettiin tutkimusalueilta, merkittiin ruumiinonteloon kirurgisesti asennettavilla radiolähettimillä ja vapautettiin pian merkitsemisen jälkeen takaisin pyyntialueilleen. Kaloja tarkkailtiin antennin ja vastaanottimen avulla kerran päivässä päiväaikaan joko rannalta tai veneestä. Kalojen käyttämä habitaatti määritettiin kalapaikoilta maastomittauksin (IV, V) tai virtaamamallin avulla (VI). Saatavilla oleva habitaatti määritettiin virtaamamallin avulla (V, VI). Molemmilla tutkimusjoilla seurannassa oli kaksi kalaryhmää: Kemijoessa ryhmä 1 elokuun puolivälistä syyskuun puoliväliin (loppukesä; veden lämpötila 12,0-15,7° C) ja ryhmä 2 lokakuun ajan (syksy; 1,7-6,7° C), Kuusinkijoessa ryhmä 1 elokuun puolivälistä (loppukesä; veden lämpötila 14,5° C) joulukuun puoliväliin (alkutalvi; 0° C, osittainen jääpeite) ja ryhmä 2 huhtikuun puolivälistä (lopputalvi; 0° C, paksu jääpeite) heinäkuun alkuun (keskikesä; 19° C). Harjukset olivat varsin paikallisia kunakin vuodenaikana, pysytellen keskimäärin alle 100 m pituisella jokiosuudella kesällä, syksyllä ja talvella sekä alle 200 m jokiosuudella kutuaikana. Kalojen havaintopäivien välillä liikkuma nettomatka oli joka vuodenaikana keskimäärin alle 30 m. Harjukset kuitenkin siirtyivät pidempiä matkoja (yleensä 0,5-5 km) vuodenaikojen vaihtuessa. Syys-lokakuussa sekä Kemi- että Kuusinkijoella kalat siirtyivät kesäalueilta useimmiten alavirtaan hitaasti virtaaville jokiosuuksille. Kuusinkijoessa, jossa kaloja seurattiin aina talveen asti, osa kaloista siirtyi veden jäätymisen alkaessa alun perin valituilta suvantoalueilta toisiin suvantoihin mahdollisesti juuri jään vaikutuksesta. Keväällä jäiden lähdön aikaan, huhti-toukokuun vaihteessa, harjukset siirtyivät talvehtimissuvannosta useimmiten ylävirtaan potentiaalisille kutualueille. Kutukauden päättyessä osa kaloista siirtyi kesäalueille, joskin noin puolet kaloista vietti kutukauden ja kesän samalla alueella. Kesällä ja kutuaikana harjukset käyttivät selvästi matalampia, nopeavirtaisempia ja isokivisempiä mikrohabitaatteja kuin syksyllä ja talvella. Jokijaksotasolla kalojen valitsemat paikat erosivat vuodenaikojen välillä siten, että kesällä ja keväällä harjukset olivat aina suhteellisen nopeavirtaisilla mutta muuten monentyyppisillä alueilla (mm. rännimäisessä voimalaitoksen alakanavassa, kuohuvissa koskipaikoissa ja tasaisesti virtaavissa suvantojen ala- ja yläosissa), kun taas syksyllä ja talvella ne olivat selvästi koskiosuuksista erottuvilla syvemmillä suvanto-osuuksilla.

Tämän tutkimuksen osatöiden tuloksia on mahdollista soveltaa mm. elinympäristökunnostusten ja kalastusrajoitusten suunnittelussa. On ilmeistä, että harjus tarvitsee menestyäkseen hyvin erilaisia elinympäristöjä eri ikäkausina ja eri vuodenaikoina. Tiukimmat habitaattivaatimukset harjuksella on todennäköisesti kutuhabitaatin, vastakuoriutuneiden poikasten syönnöshabitaatin ja talvehtimishabitaatin suhteen, ja näiden habitaattien saatavillaolevuuteen tulisikin siten kiinnittää erityistä huomiota. Kalastusrajoitukset voivat olla aiheellisia vesistöissä, joissa talvehtimispaikkoja on vähän ja suuri osa harjuspopulaatiosta voi näin ollen altistua pyynnille kylmänä vuodenaikana.

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