JYVÄSKYLÄ STUDIES IN BIOLOGICAL AND ENVIRONMENTAL SCIENCE
217

Jukka Syrjänen

Ecology, Fisheries and Management of Wild Brown Trout Populations in Boreal Inland Waters

JYVÄSKYLÄN YLIOPISTO

JYVÄSKYLÄ STUDIES IN BIOLOGICAL AND ENVIRONMENTAL SCIENCE 217

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Esitetään Jyväskylän yliopiston matemaattis-luonnontieteellisen tiedekunnan suostumuksella
julkisesti tarkastettavaksi yliopiston Ylistönrinteellä salissa YAA303
joulukuun 18. päivänä 2010 kello 12.

Academic dissertation to be publicly discussed, by permission of
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UNIVERSITY OF JYVÄSKYLÄ

JYVÄSKYLÄ 2010

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Cover picture: 18.10.2005 Joutsa, Rutajoki, Korvenkoski rapids, photo by Jukka Syrjänen

URN:ISBN:978-951-39-4150-5
ISBN 978-951-39-4150-5 (PDF)

ISBN 978-951-39-4146-8 (nid.)
ISSN 1456-9701

Jyväskylä University Printing House, Jyväskylä 2010

Dedicated to my dear family

ABSTRACT

Syrjänen, Jukka
Ecology, fisheries and management of wild brown trout populations in boreal inland waters
Jyväskylä: University of Jyväskylä, 2010, 43 p.
(Jyväskylä Studies in Biological and Environmental Science
ISSN 1456-9701; 217)
ISBN 978-951-39-4150-5 (PDF), 978-951-39-4146-8 (nid.)
Yhteenveto: Luontaisten taimenkantojen ekologia, kalastus ja hoito pohjoisilla sisävesillä
Diss.

Migratory fish in general, and stream salmonid stocks in particular, have suffered strongly from anthropogenic pressure throughout the world during the last century. The quality and quantity of stream environments have decreased, and overfishing has diminished the spawning stocks. The goal of this thesis was to provide new insights into different phases in the life histories of wild brown trout and into the effects of environmental and fisheries management on brown trout populations. The work aimed (i) to study the growth and emergence of brown trout embryos, (ii) to evaluate prey selection by parr in boreal stream environments, (iii) to explore the impacts of a common management action, in-stream restoration, on wild trout stocks, and (iv) to describe the current state of previously abundant stocks of lake-migrating trout in the Kymijoki water course. Embryonic growth rate and the time of hatching differed between lake outlet and downstream habitats, but emergence was predicted to take place simultaneously within a few days in all habitat types. Egg survival was high in streams of good to excellent water quality. Parr used food items mostly according to their availability, and the most important prey group was blackfly larvae. In small streams, terrestrial invertebrates were one of the most important prey groups, but only in autumn. Restoration of streams dredged in the 19th and 20th centuries modified the channel structure, making it more heterogeneous. However, no impact of restoration was detected in the abundance of wild young brown trout, which may result from the lack of moss and wood in newly restored channels, from little change to pool area, or from the small number or size of spawners. Currently, spawning trout in the Finnish Lake District are mainly local in rivers of good to excellent water quality, but they still produce some smolts to lakes. Almost all lake-migrating individuals are caught from the lakes and are therefore prevented from reproducing.

Keywords: Boreal streams; brown trout; embryo; overfishing; prey selection; stream restoration.

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following original papers, which will be referred to in the text by their Roman numerals I-IV. The idea and planning for papers I, II and IV were given by me and the co-authors. Timo Muotka gave birth to the idea in III. I organized field sampling with Anssi Eloranta in I, with Petri Kreivi and Kai Korsu in II, and with Timo Muotka in III. I contributed mainly field sampling in IV. I analyzed data with Mikko Kiljunen in I, with Pauliina Louhi and Riku Paavola in II, and with Timo Muotka in III. I did data analyses in IV. I wrote mainly manuscripts in I, II and IV. Timo Muotka wrote mainly the manuscript in III. All manuscripts were completed together with the co-authors.

I Syrjänen, J., Kiljunen, M., Karjalainen, J., Eloranta, A. & Muotka, T. 2008. Survival and growth of brown trout *Salmo trutta* L. embryos and the timing of hatching and emergence in two boreal lake outlet streams. Journal of Fish Biology 72: 985-1000.

II Syrjänen, J., Korsu, K., Louhi, P., Paavola, R. & Muotka, T. 2010. Stream salmonids as opportunistic foragers: the role of terrestrial invertebrates along a stream-size gradient. Manuscript.

III Muotka, T. & Syrjänen, J. 2007. Changes in habitat structure, benthic invertebrate diversity, trout populations and ecosystem processes in restored forest streams: a boreal perspective. Freshwater Biology 52: 724-737.

IV Syrjänen, J. & Valkeajärvi, P. 2010. Gillnet fishing drives lake-migrating brown trout to near extinction in the Lake Päijänne region, Finland. Fisheries Management and Ecology 17: 199-208.

1 INTRODUCTION

1.1 Management of boreal streams and salmonid stocks

1.1.1 Human actions in streams

In the history of human societies, streams have provided routes for transportation and power for mills and power plants, but also opportunities for food supply and recreation. Humans have modified stream channels to better fit with their socio-economic needs. In boreal zones, streams were used as routes for human movement, but also for transportation of wood. Mills and sawmills began to rise on streams, and they became numerous in the 19th century, before being later replaced by hydroelectric power stations. Thousands of dams were built for those purposes, as well as for lake regulation. Almost all forest streams in Finland were dredged for timber floating during the 19th century and the first part of the 20th century. The total length of stream channel dredged for log transport was ca. 20 000 km in Finland (Lammassaari 1990) and ca. 30 000 km in Sweden (Törnlund & Östlund 2002).

In the 1960s and 1970s, forests and bogs were ditched extensively to enhance forest production. Streams were straightened, and floods and droughts probably became more extreme as the water retention capacity of forests and bogs was weakened. Fine organic and inorganic matter sedimentation increased (Joensuu et al. 1999) and clogged the spawning gravel beds (see Laine & Heikkinen 2000). In many Finnish large lake systems, water quality decreased because sewage waters, especially from the forest industry (e.g. in Päijänne region, see Meriläinen & Marttila 1998). As a result, the physical and chemical environment for salmonids deteriorated severely in streams and in some lakes. Migration routes were partially or totally closed, and the quality and quantity of reproduction areas decreased, leading to weakened reproduction of salmonids (see Laine et al. 2001). Also many lakes were affected by forest and bog waters possibly disturbing the reproduction of vendace (*Coregonus albula* (L.)) populations, the most important prey fish for lake-migrating brown trout

(*Salmo trutta* L.) and landlocked salmon (*Salmo salar* m. *sebago* Girard) in the Finnish Lake District (Koivurinta et al. 2000).

After the last reproduction area of the landlocked salmon, the Kuurna Rapids on the River Pielisjoki, was dammed in 1971 and two large reservoirs, Lokka and Porttipahta, were built on the River Kemijoki in 1970, attitudes towards stream management in Finland started to change from destructive exploitation to restoration of dredged channels. In the 1980s, restoration activities spread through the country, driven by the regional Environment Centres. To date, thousands of kilometres of stream channels have been restored (Yrjänä 2003), and some hundreds of fishways or bypass channels have been build. It is evident that morphological diversity has increased through restoration (Huusko & Yrjänä 1997), but the management measures have not been shown to improve the stream habitat suitable for brown trout or Atlantic salmon (Korsu et al. 2010), or to increase parr density or to reinstate migratory populations (III, IV). In the Lake District, most streams are now physically in moderate-to-good condition, with open access for fish, and water quality is good to excellent, allowing natural reproduction of salmonids. However, peat mining for fuel supply seems again to be increasing in Finland, which may increase sedimentation of fine organic matter and thus weaken the natural reproduction of salmonids again.

1.1.2 Harvesting of salmonids

As salmonids are highly appreciated as human food, they have been strongly harvested almost everywhere that they occur. In the 19th century, brown trout and Atlantic salmon (*Salmo salar* L.) in Finland were mainly caught in streams with weirs/traps, hooks and gigs (Hurme 1966a). Longlines and some gillnets were used in lakes and the sea in the beginning of the 20th century, but fishing in lentic waters increased distinctly in the 1940s and 1950s as monofilament gillnets came into common use (Hurme 1966a). Harvesting in streams remained intensive, and there were practically no regulations for catching salmonids or predatory fish in general. Eventually, fishing of salmonids, including southern populations of Arctic charr (*Salvelinus alpinus* (L.)) (Salmi et al. 2000), rose to a level where fishing mortality threatened the existence of the last wild stocks that survived the damming and channelization of streams (Romakkaniemi et al. 2003). As the reproductive environments were widely deteriorated at the same time, wild populations of brown trout and Atlantic salmon, especially migratory ones, collapsed (Romakkaniemi et al. 2003). In the 20th century, even resident populations of brown trout in brooks were strongly harvested with rod and line, with no or only very loose regulations. Stocks of sea-migrating and sea-spawning grayling (*Thymallus thymallus* (L.)) collapsed in the 1930s to 1960s also in the Gulf of Bothnia, first presumably because of strong, almost unlimited harvesting, and then because of dredging and damming of spawning streams in the 1950s and 1960s. The annual catch of the Bothnian grayling was tonnes or more in the 1910s and 1920s (Hurme 1966b), but now the stock is almost extinct.

The falling catch of wild salmonids was noticed by fishery authorities and researchers in the latter half of the last century, but the adopted "cure" was neither to limit the catch nor to restore environments, but rather fish hatching and stocking (Hurme 1966a). From the 1950s onwards, the stocking of Atlantic salmon, brown trout, landlocked salmon, whitefish (*Coregonus lavaretus* (L.)), grayling and recently pikeperch (*Sander lucioperca* (L.)) has continued, but pike (*Esox lucius* L.), rainbow trout (*Oncorhynchus mykiss* (Walbaum)), brook trout (*Salvelinus fontinalis* (Mitchill)) and lake trout (*Salvelinus namaycush* (Walbaum)) have also been used. Stocking has aimed primarily to improve the catch, but not to recover the wild spawning stocks. In lakes, stocking retained the catch of the game fish and whitefish at a moderate or good level by numbers, but not by weight, as the stocked fish were and are still harvested at small size. This, however, allowed easy harvesting for local fishermen, and without fishing regulations. Wild spawning stocks were ignored in fishery politics, and hatcheries provided cheap, reared young fish. Thus, lake ranching became a constant management practice in Finland, especially in inland waters.

As the problem of overfishing of salmonids has been generally accepted in Europe and North America, fishing regulations, even ultimately strong ones, have been established. For instance, in California (USA), the sea fishing of chinook salmon (*Oncorhynchus tshawytcha* (Walbaum)) was mainly banned in 2008 and 2009 because of the fall of the wild stocks (Anon. 2009), and in the famous salmon and sea trout rivers Dee, Spey, Tay and Tweed in Scotland, new rules have forced all or most wild Atlantic salmon and sea trout to be released from 2009 onwards (Anon. 2010). In Irish lakes, gillnet fishing is totally banned (Prof. Ken Whelan, University College Dublin, personal communication). In Finland, however, the practice is different. Despite the strong harvesting, even overexploitation, of salmonids in many Finnish waters, the social awareness of the state of the last wild salmonid stocks and the effect of fishing on them seems to be low, and only a few recovery plans with conservative fishing regulations have been realized. The overall status of wild stocks as a valuable natural resource has unfortunately not improved much even in the 21st century. In the River Tana, for example, the most productive Atlantic salmon river in the world, fishing rules allow almost unlimited killing of wild spawners, for tourists by rod, but for local people also with gillnet, driftnet and weir. On inland waters, some advance has been made in the 21st century, as wild brown trout has been protected in most streams in the Kymijoki drainage. However, harvesting in lakes, mainly with gillnets, probably kills most migrating wild individuals, as is the case with stocked individuals (Syrjänen et al. 2010 a, b), but unfortunately, the state and fate of wild lake-migrating stocks is not well known in the Finnish Lake District.

1.2 The role of wild salmonids in boreal stream ecosystems: food webs and environmental limits

Salmonid fish in stream food webs act as consumers of benthic animals, which in turn use plankton, algae, organic matter or other benthic animals as their food resource. In addition, salmonid fish use terrestrial invertebrates (Wipfli 1997, Allan et al. 2003, Kawaguchi et al. 2003, Johansen et al. 2005, Baxter et al. 2007), especially in small streams where the terrestrial input of matter and energy fuels the ecosystem and benthic animals are less abundant.

At the population level, stream salmonids use prey animals roughly as they are available (Elliott 1973, Allan 1981, Dedual & Collier 1995, Lagarrigue et al. 2002, Johnson et al. 2007). Thus, stream salmonids are classified as omnivorous foragers (Klemetsen et al. 2003). However, they often prefer the largest invertebrate prey available (Allan 1981, Angradi & Griffith 1990, Laudon et al. 2005, Meissner & Muotka 2006). Individual fish can also specialize on a certain prey group, and individual variation in prey use can be high (Bridcut & Giller 1995). When larger, stream salmonids may shift partly to piscivory (Garman & Nielsen 1982, Klemetsen et al. 2003), which enhances individual growth (Garman & Nielsen 1982, Elliott & Hurley 2000). Brown trout as small as 15 cm can prey on small fish like minnows (own unpublished data). Stream salmonids themselves serve as prey for larger predatory fish, such as pike (Mann 1976, Mills 1986), burbot (*Lota lota* (L.)) (own unpublished data), and pikeperch (Jepsen et al. 2000), as well as for predatory mammals, such as otters (*Lutrinae*) (Carss et al. 1990, Crait & Ben-David 2006) and minks (*Mustelidae*) (Mills 1986, Heggenes & Borgstrøm 1988), or for predatory birds, such as mergansers (genus *Mergus*) (Wood 1987, Feltham & MacLean 1996).

Food resources often determine the growth rate of salmonid parr in streams (Cada et al. 1987, Mortensen et al. 1988, Andersen et al. 1992, Chappaz et al. 1996, Johnson et al. 2006), together with physical factors, like water temperature (Preall & Ringler 1989, Elliott et al. 1995, Elliott & Hurley 1997, Lobon-Cervia & Rincon 1998, Magoulick & Wilzbach 1998, Jensen et al. 2000, Forseth et al. 2001). This means that food availability may be the limiting factor for growth, creating bottom-up regulation. Food limitation often occurs in summer or autumn, when food abundance is low (Haapala & Muotka 1998) and water temperature is partly above the optimum. In summer, water temperature is often too high for fast growth, especially compared to the low food availability. Growth in boreal streams is negligible, even negative, in winter (Egglishaw & Shackley 1977, Budy et al. 2008), when cold water causes low metabolic activity (Cunjak & Power 1987). Thus, the best growth season in Finland is spring, from mid April to mid June (see Korsu et al. 2009), when the biomass of the main food resource, benthic invertebrates, is still high (Haapala & Muotka 1998) and temperature is near the optimum.

During the embryonic phase, abiotic factors, like temperature, water acidity and fine organic or inorganic matter, determine growth, development, hatching time (Elliott & Hurley 1998a, Elliott & Hurley 1998b, Beer & Anderson 2001) and survival (Olsson & Persson 1986, 1988) of embryos, as well as the emergence time of the alevins. During emergence, floods (Jensen & Johnsen 1999, Fausch et al. 2001) and predation (Brännäs 1995) affect alevin survival. Density-dependent mechanisms operate after emergence to regulate the growth (Jenkins et al. 1999) and survival of parr (Elliott 1987, Elliott 1989, Bujold et al. 2004). Territoriality of individuals is one of the most important drivers during the parr period (Elliott 1990, Johnsson et al. 1999, Steingrimsson & Grant 1999), decreasing the density dependence of growth. Intraspecific competition begins just after emergence (Titus & Mosegaard 1991, Bujold et al. 2004) and occurs within (Elliott 2002) and between age groups (Bohlin 1977, Nordwall et al. 2001) although habitat segregation partly reduces intercohort competition. High density of parr may induce migration behaviour of individuals due to resource limitation (space and food). In artificial stream channel experiments, low prey availability has been shown to increase the emigration of individuals (Keeley 2001, Imre et al. 2004,).

Boulder or wood installation may decrease the size of individual territories (Imre et al. 2002) and thus increase the environmental capacity for parr. Smaller territory size, however, has been shown to increase population density in only a few experiments (Venter et al. 2008).

1.3 Study objectives

The objective of this thesis was to study the ecology of stream living brown trout and the effects stream and stock management measures. The new information obtained could be used by authorities in combining fisheries and environmental management. This general objective was divided into four subtasks.

The first subtask (I) was to describe the growth patterns of brown trout at the embryonic stage, when growth and development under natural conditions is poorly documented. My aim was to compare the survival of brown trout alevins until hatching, and the timing of hatching and emergence, between two habitat types with different annual stream temperature profiles, a lake outlet and a downstream site.

The second aim (II) was to document prey use by brown trout relative to availability in benthic and drift samples in streams of different size. Furthermore, the significance of riparian prey to trout diets was determined.

The third aim (III, IV) was to overview the impacts of recent channel restoration actions in Finnish boreal streams. This management action has been very extensive, because in Finland nearly all stream channels wider than five meters have been dredged and have now been restored. Stream restoration aims at returning channels to their original physical and biological condition. Despite the quite large number of restoration projects during the last three decades, any long-term benefits of stream restoration are still largely unconfirmed.

The last aim (IV) was to describe the state of the wild populations of lake-migrating brown trout in the Kymijoki drainage basin, and the role of fishing in the current state of populations, with suggestions for possible recovery actions.

2 MATERIALS AND METHODS

2.1 Study areas

The data for the thesis derive mainly from second-to-fourth-order boreal forest streams situated in Central Finland in the Kymijoki drainage basin (Fig. 1). In II and IV, second-to-fifth-order streams in Central Finland were studied. Data from second-to-fifth-order streams in the Iijoki and Koutajoki drainage basins in northern Finland was also included in II and III. A restricted reference data set from the river Juutuanjoki in the Paatsjoki water system in northernmost Finland (Fig. 1) was used in IV. Additional data sets for fishing effort, trout size in lake catch and parr density in streams were collected from Lakes Konnevesi, Keitele and Puula in the Kymijoki drainage basin and from Lake Pääjärvi in the Koutajoki drainage basin. Furthermore, some redds were sampled from the tributaries of these lakes.

Most of the studied streams are oligotrophic or mesotrophic and mesohumic with low to moderate spring floods and a winter period of four to six months with water temperature near 0 °C. All study sites are situated less than 120 m above sea level. Brown trout reproduce naturally in all the streams, and spawners are almost totally resident, excluding Juutuanjoki and Vaskojoki, where most spawners enter the tributaries of Lake Inari. Other fish species in the studied streams are bullhead (*Cottus gobio* L.), roach (*Rutilus rutilus* (L.)), perch (*Perca fluviatilis* L.), burbot, grayling, stocked rainbow trout, bleak (*Alburnus alburnus* (L.)), minnow (*Phoxinus phoxinus* (L.)), ruffe (*Gymnocephalus cernuus* (L.)), stone loach (*Barbatula barbatula* (L.)) and pike.

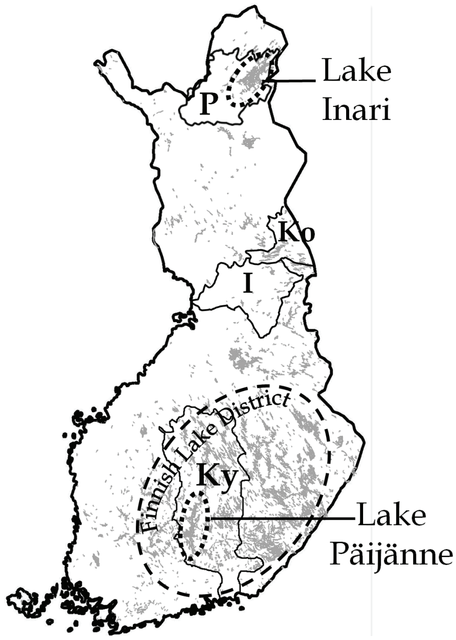

FIGURE 1 Location of the Finnish Lake District and the studied water courses. Kymijoki (Ky), Iijoki (I), Koutajoki (Ko), and Paatsjoki (P) drainage basins, and Lakes Päijänne and Inari.

2.2 Survival and growth of brown trout embryos and the timing of hatching and emergence (I)

Two streams and two habitat types, a lake outlet and a downstream site, were used to monitor stream temperature, and survival and growth of embyos and timing of hatching during seven winter/spring months. Lake outlet and downstream sites were chosen because of their different expected stream temperature profiles.

Cylinder-shaped egg containers made of plastic net were used to monitor the egg survival and embryonic growth. Fifty brown trout eggs were mixed with gravel in each cylinder. Cylinders were then placed in plastic baskets, four to six cylinders in each basket. Five or six baskets were used at each study site. The baskets were buried in gravel beds. Upon sampling, one cylinder from each basket was lifted randomly, and dead embryos, living hatched embryos and living unhatched embryos were counted. In the laboratory, yolk and body were separated and weighed and the total length of each fish was measured.

The model of Elliott & Hurley (1998c) was used to predict the timing of emergence from gravel. The model was validated by comparing the observed and predicted hatching times. Because eggs were fertilized and placed in the incubation sites simultaneously, the average hatching and emergence intervals could be predicted using water temperatures monitored during the experiments. Given a single fertilization date, the number of days required for 5, 50 and 95 % of eggs to hatch was estimated using equations of Elliott & Hurley (1998c). To validate the modelled hatching dates, the time required for 5, 50 and 95 % eggs to hatch was estimated from the experimental data by probit analysis (Finley 1971). For growth differences during the winter, a two-way ANOVA was performed for the mean dry mass of body and yolk, as well as for embryo length in mid March, with river and habitat type as the main factors. Differences among rivers (Arvaja v. Rutajoki) and habitat types (outlet v. downstream) in the proportion of hatched embryos at the time of the last simultaneous observation (mid April) were also tested by two-way ANOVA on arcsin-transformed data. Two-way ANOVA was used in a similar way to test for embryo survival and size in mid April.

2.3 Prey preference patterns and the importance of terrestrial prey (II)

Two data sets were used: field material was collected from 25 streams to assess prey preference of brown trout and a literature survey was used to quantify the importance of terrestrial invertebrates in the diets of stream salmonids.

The sampling focused on late summer to early autumn (August to September) when all 25 streams were sampled, but to assess the seasonal variability in trout diets, seven streams were also sampled in early summer (early June). The studied streams were divided into three size-groups: small (mean channel width < 3.5 m, n = 10), medium-sized (4-12 m, n = 8) and large (20-80 m, n = 7). Trout of mainly 11-22 cm total length were collected by electrofishing, anaesthetized, and their stomachs were flushed with 3-4 dl of water. Prey availability in the benthos was measured by collecting kick net samples and prey availability in the drift was measured using PVC tube samplers.

Prey taxa were grouped into eight functionally and/or taxonomically similar groups that dominated in the benthic/drift samples or trout diet: baetid mayfly nymphs, non-predatory stonefly nymphs (mainly families Leuctridae and Nemouridae), case-bearing caddis larvae, net-spinning caddis larvae, chironomid larvae, blackfly larvae, adult stages of aquatic insects, and terrestrial invertebrates. Prey availability was compared to prey consumption using Chesson’s (1983) preference index separately for benthic and drift samples.

Rader (1997) classified aquatic invertebrates based on 11 traits that determine their availability to salmonid fishes. He assigned each prey to each of these categories, using scores from 0 to 9, then summing the subtotal group scores. For final group scores, subtotal scores were weighted by multipliers depending on the abundance of each prey. To test the applicability of Rader’s model to our data, exactly the same prey groups and scores were used as in Rader (1997) for all prey taxa that occurred in our data. Spearman rank correlations were used to test for the correspondence between trout diet and several measures of prey availability: (i) diet composition (proportional abundance of each prey type) vs. Rader's (1997) scores; (ii) diet vs. Rader's scores combined with site-specific abundance in benthic samples; (iii) diet vs. relative abundance in benthos; (iv) diet vs. Rader's scores combined with site-specific abundance in drift samples; and (v) diet vs. relative abundance in drift. Only those eight of Rader's original traits that characterize aquatic life forms/stages were used.

Nonmetric Multidimensional Scaling (NMDS) ordination was used to compare visually patterns in trout diet vs. benthic samples, and Procrustes analysis with ProTest was then made to test for pairwise concordance among the two ordination configurations. Differences in community composition among stream-size classes, separately for dietary and benthic samples, were analysed by Multi-Response Permutation Procedure (MRPP).

To quantify the general importance of terrestrial invertebrates to the diet of stream salmonids, a literature survey was performed using Biological Abstracts and Google Scholar™ using key words: 'trout', 'salmon', 'charr', 'food', 'feeding', 'diet', 'foraging', 'prey', 'predation' and 'terrestrial'. Our own data (II and unpublished) were added to the final database. For each study, the percent of terrestrial invertebrates (aquatic adult insects not included) was recorded in the diets of salmonids, as well as several explanatory variables: channel width, fish size-class, salmonid genus, and riparian vegetation type. Individual streams were considered as data points (replicates), but if a study reported information on several fish size-classes, fish genera and/or riparian vegetation type, each was included as a separate data point. Data were analyzed using generalized least squares model (GLS).

2.4 Channel restoration and its consequences for stream biota (III)

The review paper focuses on hydromorphological and functional effects of channel restoration, and its success in increasing parr abundance in Finland. Different designs were presented for different topics, and details are given in Muotka & Laasonen (2002) and Muotka et al. (2002)). In previously unpublished material, snap-shot data were used for channel morphology on both patch and reach scale, with BACI-design (Before, After, Control, Impact) of one impacted stream or BA-design with one or three impacted streams included. For brown trout abundance, two temporally replicated BACI-designs were used, with one or two impacted streams and monitoring period of ten and eight years, respectively.

Channel morphology was measured with different methods. At a patch scale (0.1-1 m) in the stream Myllykoski, a bed profiler was used to quantify streambed roughness. In addition, FST-hemispheres were used to quantify changes in shear stress (N cm^{-2}) following Statzner & Müller (1989) at a sampling window of 10 m × 9 m in 100 regularly spaced spots. The procedure was repeated before and after channel restoration. At the reach scale, the proportion of different channel units (riffles, runs, pools) was estimated in the streams Rutajoki, Könkköjoki and Myllykoski. For each stream, the same reach (300–1000 m) was surveyed both before and 2 years after restoration. At the drainage scale, detailed habitat surveys were conducted for 30 streams divided into six groups according to their management state (natural, channelized, or restored 1 month or 4, 6 or 8 years before sampling), described in detail by Muotka et al. (2002). A detailed comparison was made between a third-order forest stream (Kosterjoki) in northeastern Finland, before and after its restoration, and a close-to-pristine reference stream in an adjacent catchment. A retention experiment was conducted with artificial plastic leaves just before and 3 years after restoration in a 50-m long study section in each stream (Muotka & Laasonen 2002).

To estimate parr abundance, electrofishing was carried out with three-pass sampling. The total sampling area was 150-400 m^2 per site. Fish number per sampling was estimated with formulas given by (Junge & Libosvarsky 1965) or (Bohlin et al. 1989). As apparent catchability could be used only for a few sampling areas and occasions, stream-level catchability for all years combined was used for brown trout, perch and roach and, in some cases, for bullhead. For other species, whole-data catchability was used. Catchability was thought to be high enough to allow comparison of brown trout and other species abundances between sites with the three-pass method. Average catchability in the whole data set (II, III and IV) was 0.52 for 0-year-old trout, 0.63 for older trout, 0.34 for bullhead, 0.66 for roach, 0.56 for perch, 0.69 for pike and 0.50 for burbot.

Two-way ANOVA was used to analyze change in stream bed roughness due to channel restoration, and an asymmetrical ANOVA to detect a possible impact on trout abundance (Underwood 1992). At the drainage scale, discriminant function analysis used as described in Muotka et al. (2002).

2.5 Lake-migrating stocks of brown trout in the Lake Päijänne region (IV)

The aim was to estimate the current status of migratory brown trout stocks in the Lake Päijänne region. Seven streams were used, and mainly snap-shot material was used for redd data, and temporal data set periods of 10-24 years were used for parr data.

Smolt numbers for the tributaries of Lake Päijänne were approximated by apparent survival between parr age groups. As part of the older parr could not be sampled effectively by electrofishing, the apparent survival between years (autumn to autumn) was estimated for all age groups from 0 to 4 samples from smaller streams Köhniönpuro and Kiertojoki. The total number of parr in the older age groups was estimated from the observed number of young-of-the-year by multiplying this by the apparent annual survival values and by the riffle surface area. The 'missing' part of older parr in electrofishing samples was computationally set to live half in streams outside the sampling areas and half in lakes as smolts.

The migration of smolts was studied by marking 1- to 4-year old wild parr with Carlin tags. Fish were collected by electrofishing in the three Päijänne tributaries. In 1999-2007, altogether 1538 parr were marked. The direction and distance of migration, catch size and the proportion of different fishing gears to the catch were recorded.

When sampling trout redds to survey the structure of the spawning stocks, riffle areas of tributaries to Lakes Päijänne, Keitele and Puula were determined by wading across the channels. In tributaries of Lakes Inari and Pääjärvi and the outlet of Lake Konnevesi, wading was carried out from shores to the depth of 1 m. This method excludes sampling in deeper areas, but it should give a reliable estimate of the size of the spawners. Length was measured separately for pot and tail of redds. As the redd tail length correlates with female length (Crisp & Carling 1989), redds were divided into large and small to estimate the number of larger migratory spawners. The threshold redd length was set at 2.5 m or 3 m in the three tributaries of Lake Päijänne (Rutajoki, Muuramenjoki and Arvajanjoki), where the largest resident fish have been observed to be 40-50 cm long. The area sampled in the three rivers was 50-80 % of the total riffle area. The density of eggs in each sampling area was estimated by the formula given for female length vs. redd length (Crisp & Carling 1989) and for egg number in redd vs. female length (Elliott 1995), and the total number of small and large redds was estimated for each stream by multiplying the number by riffle surface area. A large redd was considered to result from the spawning of one or two migratory trout, and the total number of large migratory spawners was then estimated for each stream.

The Kolmogorov-Smirnov test was used to compare redd length distributions in the tributaries of Lake Päijänne and Lake Inari.

3 RESULTS AND DISCUSSION

3.1 Survival and growth of brown trout embryos and the timing of hatching and (I)

In the egg incubation experiment, water temperature determined embryonic growth and hatching dates of salmonids. Hatching intervals predicted by the Elliott & Hurley (1998c) model fitted the observed intervals reasonably well. In the outlet of a large lake, trout alevins hatched in early March, 3-4 weeks earlier than in the other incubation sites. This was because of warmer (ca. 1 °C higher on average) stream water during winter in the outlet of a large lake than in the other sites. Embryonic growth followed the same pattern, as growth was clearly fastest in the outlet of the large lake in winter. However, in spring, water temperature rose rapidly in the other study sites which accelerated alevin growth compared to the outlet site. Thus, emergence of alevins was predicted to occur at the same size and almost simultaneously within a short time period at the end of May at all sites. According to our results, alevins began active swimming, external feeding and intensive growth in May-June, and trout at the outlet of a large lake did not obtain any head start for their first summer. Our field observations of the emerged alevins matched well the predicted timing of the emergence.

According to our results, the better growth of yearlings and parr in lake outlets reported earlier for both brown trout (Jonsson & Sandlund 1979, Haraldstad et al. 1987) and Atlantic salmon (Lund & Heggberget 1985, Einarsson et al. 1990) would not result from differences in the embryonic growth or emergence times between study sites. Degerman et al. (1996) reported ca. 10 % higher maximum and minimum lengths of brown trout at the age of 0+ in Swedish lake outlets compared to other stream sections, but only from August onwards. When benthic prey biomass falls to its annual minimum during summer, food supply may begin to limit trout growth even in more unfavourable stream sites. Lake outlets, however, provide an abundant food supply even then (Richardson & Mackay 1991, Friberg et al. 2001), creating the growth difference for parr between outlets and non-outlets.

During our incubation experiments, survival of the embryos was remarkably high, 83–98 % in all sites throughout the experiment until hatching. The high survival of embryos, and the low amount of inorganic fine matter and organic matter in the egg containers support the view that the natural reproduction of brown trout can be successful in these streams typical of the Finnish Lake District streams.

3.2 Prey preference patterns and the importance of terrestrial prey (II)

Across all 25 streams (10 small, 8 medium-sized and 7 large streams), blackflies and case-bearing and net-spinning caddis larvae were the most important prey groups in trout diet in autumn. In small streams, diet was dominated by terrestrial invertebrates, blackflies and case-bearing caddis, but only cased caddis were significantly preferred by trout. In medium-sized streams, no prey type was strongly overrepresented in trout diet, except cased caddis that were again significantly preferred by trout. In large streams, trout used mostly case-bearing and net-spinning caddis and larval blackflies. In streams where drift was sampled, no consistent preference for any prey type was detected. In early summer, the most important prey group in trout diet, as well as in benthic and drift samples, was larval blackflies. Blackflies are considered as keystone organisms in boreal streams, having the capacity to transfer energy from mainly lake-derived microparticles to higher trophic levels, like stream salmonids (Malmqvist et al. 2004)

In the NMDS ordination plots, a stream-size gradient was evident, both for benthos and for trout diet. The two ordination configurations were strongly concordant, i.e. trout gut contents closely resembled benthic communities in their taxonomic composition. According to MRPP, the difference in taxonomic composition between stream-size classes was significant for diet samples whereas it only bordered on significance for benthic samples.

In our diet data, the proportion of terrestrial items in trout guts was low, being 1.1 (SE of the mean 0.2) % in small and 1.1 (0.1) % in medium-sized streams in early summer. In late summer, the corresponding values were 14.8 (7.4) % for small, 9.6 (4.9) % for medium-sized, and 2.2 (0.9) % for large streams.

Rader's (1997) model with eight invertebrate traits predicted the prey use by brown trout moderately well in the early summer. For small streams, the average Spearman correlation across all five streams in the June samples was 0.446. The average correlation r_s was lower for Rader’s scores with site-specific abundance in either benthic (mean r_s = 0.409) or drift samples (0.348). Pure availability produced the best predictions of trout diet (mean r_s for benthic samples = 0.761, mean r_s for drift samples = 0.671). In mid-sized streams in

June, correlations showed the same pattern as for small streams, with pure proportional abundance providing the best fit with trout diet. Rader's model was less successful in predicting the autumnal prey use, correlations between trout diet and unmodified Rader's scores, or scores combined with site-specific abundances, average ranging between 0.150 and 0.374. With one exception, no more than 50 % of correlations were significant. By contrast, pure availability provided in all cases a significant fit with the observed diet, average correlations ranging from 0.512 (drift abundances in a mid-sized stream) to as high as 0.654 (drift abundances in a small stream).

Altogether 41 articles were found where the proportion of terrestrial food consumed by stream salmonids was given, and these studies produced 95 data points. After adding our own data, the sample size was 122, representing stream-living populations of three salmonid genera: *Salmo*, *Oncorhynchus* and *Salvelinus* from four continents: Europe (n = 51 data poins), North America (43), Japan (12) and New Zealand (16). The overall mean proportion of terrestrial prey in salmonid diets was 17 %, indicating the importance of the group in diet as some authors have emphasized (Nakano & Murakami 2001). All other explanatory variables but stream size differed significantly among the levels included. Fish size was strongly related to the proportion of terrestrial prey in salmonid diets, with the proportion increasing from the mean of 12 % in the smallest (< 80 mm) to 25 % in the largest (≥ 150 mm) size class. The genus *Salmo* consumed less terrestrial prey (mean 9 %) than did the genera *Oncorhynchus* (27 %) and *Salvelinus* (23 %). The proportion of terrestrial prey was highest in streams flowing through deciduous forests (30 %) and lowest in coniferous forests and non-woody vegetation (11 % both).

Only one interaction was significant (Vegetation type x Salmonid genus), reflecting the fact that a great majority of studies including *Salmo* species were conducted in strongly forested watersheds. Also the interaction between riparian vegetation type and stream width bordered on significance, possibly indicating that stream width was only important in relatively small streams with mainly deciduous canopies.

The effect of stream width was obscured by the surprisingly low importance of terrestrial items in the smallest streams (i.e. less than 3 m wide). Focusing on streams wider than 3 m, a distinct size gradient was established, with the proportion of terrestrial prey in diet decreasing with increasing stream size. However, in linear regression, this gradient bordered on significance for the largest fish, as also indicated by a significant Channel width x Fish size interaction (for data excluding the smallest streams).

3.3 Channel restoration and its consequences for stream biota (III and IV)

In channel morphology assessment on a small scale, bed profile in a restored stream, but not in reference streams, changed substantially before and after restoration. Restoration clearly increased bed heterogeneity. FST measurements showed that the proportion of microhabitats with low shear stress increased after restoration. Thus, it was concluded that small scale habitat complexity increased after restoration, as did the availability of microhabitats characterized by low shear stress. On a reach scale, the proportion of runs decreased and that of riffles increased following restoration, while little change was observed in the proportion of pool habitats. It thus appears that the addition of boulders and cobbles to low-turbulence run habitats changes these to more turbulent riffles.

In the discriminant function analysis, the first axis represented a gradient in moss cover, with endpoints of high-cover natural and reference streams and low-cover recently restored streams. The second axis was related to streambed complexity; channelised streams with low bed roughness differed sharply from all other sites. Moss cover increased steadily with the recovery time from restoration, and streams restored 8 years before our survey supported a dense moss cover. A comparison between the stream Kosterjoki before and after its restoration revealed mainly positive changes in habitat structure: a uniform depth distribution shifted to a much more complex one and the velocity distribution shifted towards slow-velocity habitats, both resembling those of the unmodified reference stream. Undesirably, however, moss cover declined to one-tenth of the pre-restoration level. This phenomenon has been repeatedly observed in Finnish streams after restoration (Laasonen et al. 1998, Muotka et al. 2002, Korsu 2004). We therefore recommend that heavy machinery and procedures that destroy mosses should be reconsidered in the future. Leaving areas of stream bed intact during restoration could accelerate re-colonization by mosses.

In the stream Rutajoki, the average density of brown trout of the age 0+ was slightly lower after restoration, but the decreased abundance was non-significant. In Könkköjoki, trout density increased after restoration compared with the reference streams, and the time × location interaction approached significance, indicating a weakly positive response of trout populations to restoration. Densities of age-groups 1 and 2 showed no change in response to restoration in either of the two restored streams. Other fish species in the study streams were either very rare or did not show any responses to channel alteration. Monitoring of trout populations was continued in 2004-2008 in all streams (IV), but no increase in trout abundance was detected in the restored streams in comparison to reference streams, until the protection of wild trout (catch and release fishing from 2005 onwards) in Rutajoki, Könkköjoki and Muuramenjoki. Then, trout density rose from about 10 to about 20 individuals

100 m^{-2} in both Rutajoki (IV) and Könkköjoki (own unpublished data) between 2006-2008, but no rise was seen in Muuramenjoki (IV).

It was concluded that the lack of response of trout densities to stream restoration measures is due to only modest changes in those stream habitat structures important for trout, especially the fact that the amount of pool habitats did not increase. Pools with abundant woody debris are key features of salmonid habitats in summer (e.g. Bridcut & Giller 1993, Urabe & Nakano 1998, Rosenfeld et al. 2000) and even more so in winter (Cederholm et al. 1997, Jakober et al. 1998, Harvey et al. 1999). If, as suggested by many authors (Cunjak 1996, Quinn and Peterson 1996, Mäki-Petäys et al. 1999, Solazzi et al. 2000), winter represents a bottleneck for the survival of juvenile salmonids in boreal streams, restoration schemes aiming at enhancing trout survival and production should ensure the provision of suitable overwintering habitat (Cunjak 1996). Although some studies have shown a positive effect of stony enhancement structures on trout populations (Näslund 1989, Linlökken 1997), adding wood to streams devoid of large woody debris is probably a more effective short-term management option. Stewart et al. (2009) showed in their meta-analysis, that in-stream devices may increase population size of stream salmonids in small streams, but these devices were large woody structures in most study streams. In a literature survey of 211 restored streams or stream sections, different in-stream structure types were equal in their effectiveness to increase salmonid abundance, but the positive impact on brown trout was small compared to the average of seven species or forms and the impact was smallest on the smallest fish length class (< 10 cm) (Whiteway et al. 2010).

Another reason for the lack of restoration response may be that the size of the spawning stock functions as the limiting factor for parr abundance. Furthermore, the size of spawning stock and egg and alevin production may be limited by fishing mortality in streams and lakes (IV). Louhi (2010) assumed, that the lack of positive impact on restoration of North-Ostrobothnian rivers could result from the fact, that the historical channelization of streams affected only partial loss in habitat heterogeneity, or that changes in regional land use affect watersheds and streams more strongly than local channel management.

Retention efficiency in the reference streams was high, with 60–70% of the 2000 leaves released being retained within a 50-m study section (Muotka & Laasonen 2002). By contrast, channelised streams were poorly retentive (c. 10% of leaves retained), and the increase in the retention capacity after restoration was modest. Aquatic mosses were the key retentive feature in both channelised and natural streams. The loss of mosses during restoration works may have far-reaching effects on stream ecosystem dynamics. Mosses trap organic material and provide a rewarding feeding arena for aquatic insects (Suren & Winterbourn 1992, Lee & Hershey 2000). Furthermore, mosses are used extensively by juvenile brown trout as underwater cover (Mäki-Petäys et al. 1997, Heggenes & Saltveit 2002).

3.4 Lake-migrating stocks of brown trout in the Lake Päijänne region (IV)

In spawning redd monitoring altogether 176 redds were observed in Rutajoki (9 years of monitoring), 17 in Muuramenjoki (3) and 12 in Arvajanjoki (1). The annual range was 10-28 redds in Rutajoki and 4-8 redds in Muuramenjoki. Of all redds, 6 in Rutajoki were 3 m long or more. In addition, 7 redds were 2.5-2.9 m long in Rutajoki and 2 in Muuramenjoki. The average redd length was 1.4 m in Rutajoki (range 0.5-4.4 m), 1.6 m in Muuramenjoki (0.7-2.9 m), and 1.0 m in Arvajanjoki in 2007 (0.4-2 m). Average egg density was 4 eggs m^{-2} (inter-annual range 1-8) in Rutajoki, 2 (2-3) in Muuramenjoki and 1 in Arvajanjoki. If redd threshold length was set at 3 or 2.5 m, the annual average number of large spawners was 1-2 or 3-6 fish in Rutajoki, and 0 or 1-2 in Muuramenjoki, and none in Arvajanjoki. The redd length distribution differed between tributaries of Lakes Inari and Päijänne. In Lake Inari tributaries, redds were longer and larger. Mean redd length was 3.3 m (range 1.8-5.8 m, n = 19) in Juutuanjoki and 2.5 m (1.8-3.9, n = 11) in Vaskojoki.

The results show an almost total lack of migrating fish in the best spawning areas in the Kymijoki water course. Redds considered large were mainly around 3 m long, indicating that the few possible migrating spawners were small, likely first-time spawners. In addition, although redds in River Juutuanjoki and its tributary were roughly twice as long as in the Kymijoki water course, the state of the wild migrating stocks in Lake Inari is far from natural: brown trout is heavily harvested in the lake, as the catch for wild trout is c.a. 25 tonnes annually (Salonen et al. 2008), amounting to 7 000-15 000 individuals. Thus, most spawners in the tributaries of Lake Inari are probably first-time spawners. Without fishing mortality in the lake, the average redd length could be substantially higher than at present.

By January 2008, altogether 21 tag returns had been registered from wild smolts marked as parr (n = 1583). Brown trout in River Rutajoki had produced 16 returns, Muuramenjoki had produced two returns and Arvajanjoki three returns. All Rutajoki fish and one Muuramenjoki were taken in Lake Päijänne and one Muuramenjoki and one Arvajanjoki fish from the upstream lakes of the rivers. Four of the individuals caught were longer than 49 cm, and only the largest fish (69 cm long male) was caught as a lake-returning mature fish in its home stream. Of Rutajoki trout, 12 fish were captured within 25 km from the river mouth. The information about fishing gear was obtained from 15 fish: 9 trout were taken with gillnets and 6 with rod, of which 2 were released. Recent catch information of stocked trout is similar: gillnet is the main gear in trout harvesting (Syrjänen et al. 2010 a, b). It is evident that gillnet fishing regulation, if it is ever to occur, will be the key factor in the recovery measures for wild trout.

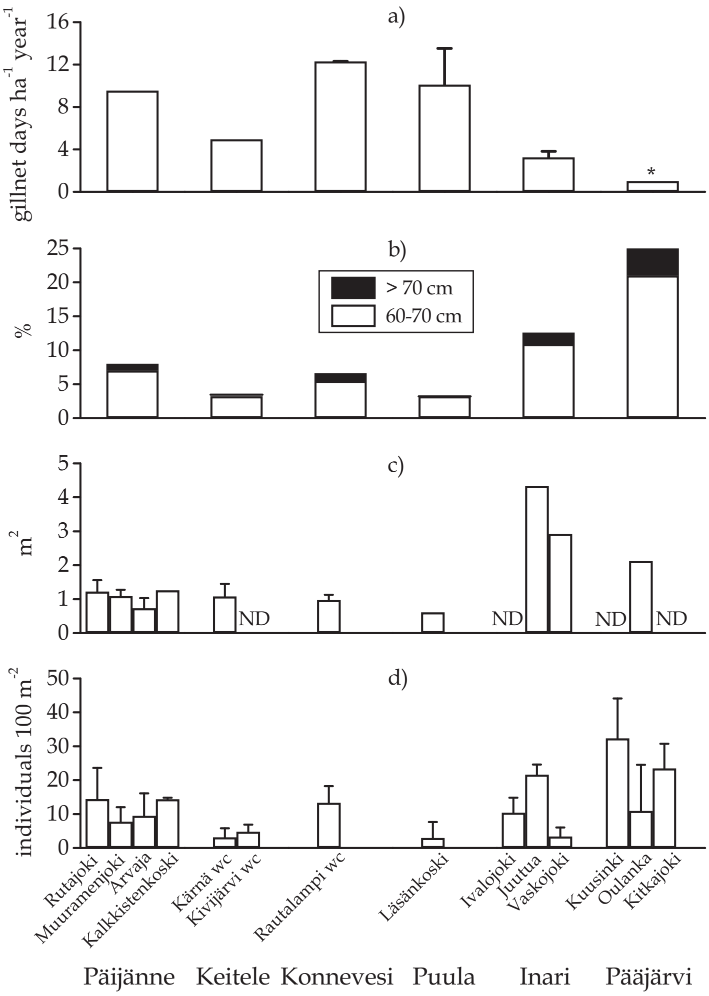

FIGURE 2 Averages of annual means for (a) gill net fishing pressure, (b) proportion of large brown trout in lake catch, (c) surface area (m^2) of brown trout redds and (d) parr abundance in four large lakes and their inlets or outlets in Kymijoki drainage basin and in Lakes Inari and Pääjärvi drainage basins in 1996-2008. Error bars represent 1 SD across years. wc = watercourse, ND = no data. All channels in the four Kymijoki lakes are restored. Egg stocking have been done in Kalkkistenkoski and Rautalampi wc. * = lower than in Lake Inari (Dr. Ari Huusko, Finnish Game and Fisheries Research Institute, personal communication). Data from Valkeajärvi & Salo (2000), Salo & Valkeajärvi (2006), Valkeajärvi (1993), Marjomäki et al. (2001a), Marjomäki et al. (2001b), Salonen et al. (2005), Salonen et al. (2007), Salonen et al. (2008), Valkeajärvi et al. (2010), Syrjänen et al. (2010a), Dr. T. Niva, Finnish Game and Fisheries Research Institute (unpublished), Docent A. Huusko, Finnish Game and Fisheries Research Institute (unpublished), own unpublished data, Ph. Lic. P. Valkeajärvi, Finnish Game and Fisheries Research Institute (unpublished), Docent T. Marjomäki, University of Jyväskylä (unpublished), Fishery Advisor J. Jokivirta, Keski-Suomen Kalatalouskeskus (unpublished).

The reported level of gillnet fishing effort was 10-12 net days ha^{-1} $year^{-1}$ in Lakes Päijänne, Puula and Konnevesi, but only 5 days in Lake Keitele (Fig. 2a). The proportion of large trout (≥ 60 cm) in the lake catch was low, 4-8 % (Fig. 2b) describing the low proportion of mature individuals in the southern lakes. As wild smolts are most likely few and harvested before reaching maturity, migratory spawners are sparse, and redds are small (average area c.a. 1 m^2) (Fig. 2c) and almost certainly dug mainly by resident spawners. Parr numbers are still low or moderate (1-14 individuals 100 m^{-2}) (Fig. 2d) in channels restored 2-20 years ago, even though they have good or excellent water quality. In lakes Inari and Pääjärvi, gillnet fishing effort was lower (3 net days ha^{-1} $year^{-1}$ or less) and the proportion of large individuals in the lake catch was higher (13-25 %). In these water systems, redds are clearly larger (average 2-4 m^2) (Fig. 2c), small redds do not exist, and parr numbers are moderate to high (5-30 individuals 100 m^{-2}). In Lake Pääjärvi, sampling in late summer mainly missed that year's spawning stock (Doc. Ari Huusko, Finnish Game and Fisheries Research Institute, personal communication), as spawners begin their long return migration in summer. Thus, the proportion of large individuals in the lake catch (25 %) might be underestimated. In addition, this value may underestimate the proportion of mature individuals, as the minimum length for spawners in River Oulankajoki is 50 cm (Saraniemi 2005). This is lower than the minimum length of females in the southern streams Huopanankoski (56 cm) and Läsänkoski (59 cm) a century ago (Järvi 1936 a, b). The strongest spring floods occur in the streams Ivalojoki and Vaskojoki, tributaries of Lake Inari, and Oulankajoki, a tributary of Lake Pääjärvi, possibly decreasing the survival of eggs and alevins. These streams had the lowest parr abundance among the northern streams.

In Finland, the importance of sport fishing has increased while subsistence fishing with gillnets has slightly decreased during the past years (Moilanen 2009), but the aim of reaching ecological sustainability especially in lake fisheries seems very challenging (Salmi et al. 2000). The slow progress in regulatory management steps may prevent other recovery measures, like stream restoration (III) and building of fish-ways, from having any positive biological effect on the wild stocks. The ownership of Finnish waters is highly fragmented, which makes the fisheries management difficult in regional perspective. However, the capability of Finnish inland fisheries systems to solve the conflicts between versatile benefits of different stakeholders (e.g. gear regulations for protecting migratory fish) are beyond the scope of this work, but the issue would urgently need a management-research project to be launched.

The consequences of overfishing have been compensated from the 1960s onwards with large stocking also in those water systems that have remained in a moderate condition for salmonids to reproduce naturally. In inland waters, much more money is allocated to salmonid stocking than to monitoring or recovery projects of wild stocks. In recent years, however, in two Baltic rivers, Tornionjoki and Simojoki, natural reproduction of Atlantic salmon has just reached the level where the stocking of parr and smolts could have been stopped (Romakkaniemi 2008).

4 CONCLUSIONS AND FUTURE RESEARCH PERSPECTIVES

Finland is the country with the third lowest population density in Europe after Iceland and Norway, but despite this its water courses and fish resources have been historically strongly utilized, and are still being strongly managed. Most streams have gone through many utilization and management phases, including channel dredging and restoration (III), so that natural stream channels are virtually non-existent in the country. Almost free and unregulated fishing was adopted at the time of poverty during World War II, and was accentuated later by massive fish stocking in all waters, excluding the northern border regions. In inland waters, this ranching procedure has been going on with little criticism until recently (IV), although public interest in the quality of aquatic ecosystems has been rising. At the same time, more than half of medium-sized and large streams have been restored, and water quality has improved in many previously polluted waters. Nevertheless, wild migratory fish populations remain weak in the whole country, excluding the northern rivers Tana, Näätämö, Tornionjoki and Koutajoki, and the Lake Inari region.

Stream management in Finland during the last decade has concentrated on channel restoration (III). However, in the worst-case scenario, the direction of management may change again in the future, as the energy supply of human societies is changed to renewable production. Almost certainly channels will be managed throughout this century – they will be restored several times, or altered for some other purpose. What will be the ecological goals and terms for stream channel management in the future?

Many totally or partially migratory salmonid species, like brown trout, are flexible in their life cycle and ecological requirements by, for example, enduring months at a temperature of 0 °C (I) and being omnivorous in prey use (II). They can live in non-pristine environments, if migration routes are accessible and reproduction and migration areas are in good-to-moderate condition. However, as migratory species have complex life cycles and, in the north, high lifespans before reproduction, they cannot endure high fishing mortality without considerable risk of population extinction or genetic changes. In the Finnish inland fisheries, and especially in fishing tourism, brown trout is one of the most valued species (Airaksinen et al. 2006). The potential of wild stocks is much higher than the state of stocks now, but as trout are strongly harvested, mainly as a by-catch in almost unregulated lake fishing, the potential cannot be reached (IV).

Stream management, extensive fish stocking and high harvesting rates would urgently need more rigorous monitoring for the impacts of the management procedures and of the stocks themselves. Stream restoration projects still rarely include any valid monitoring programs. Even if included, monitoring is often of short duration and spatially restricted. As restoration will continue through the coming decades and will be moving towards the numerous dredged small streams (channel width < 4 m), restoration success should be monitored as field experiments with reasonable monitoring time and rigorous study designs (Roni et al. 2005). In restoration realization, the importance of restoring stream ecosystem functions and processes, including terrestrial-aquatic linkages, cannot be overemphasized.

Small channels that will be targeted by restoration in the coming decades, need to be treated with caution, however: part of these channels hold wild resident brown trout populations. Although the fishery value of these small populations is not high, they are the almost the only genetically original brown trout populations left in the country, perhaps in addition to the Lake Inari region (Swatdipong 2009) and the tributaries of the River Koutajoki, as all other populations have been mixed by stocking. Moreover, the only naturally reproducing alien salmonid in Finland, brook trout, prefers the same environment, i.e. small channels. This situation raises an important question: will restoration in the future be able to preserve and enhance the last original brown trout stocks through habitat enhancement or will it only make streams more suitable for brook trout, further enhancing its spread (see Korsu et al. 2010)? This emphasizes a re-consideration of management goals and the importance of biological monitoring in restoration projects especially in stream systems that already hold naturally reproducing alien species.

The recent documentation of a probable change in brown trout spawning stocks in the Kymijoki drainage basin during the last century from a migratory to a resident one (IV) gives an undesirable example of a phenotypic, if not genetic, alteration in the life cycle of a heavily harvested species. As parr density probably fell during the 20th century because of high fishing mortality of migrating females, food availability for and, consequently, growth of parr may have been enhanced, and females now have better resources to mature as residents. Clearly, without sufficient stock monitoring included in the fishery politics, sustainable and rational management of stocks or their environments can hardly be reached.

Only long-term monitoring could give real information about the state of the stocks and success of management. The Päijänne region is included in the international LTER network (Long Term Ecological Monitoring), but so far the network in Finland has no financial resources for monitoring – a problem all too common in research into wild fish stocks in inland waters. However, problems in salmonid management are not restricted to this fish group alone, as lake ranching possibly has effects on other predatory or long-lived fish species, like pike-perch, pike, burbot, eel, whitefish or bream. Information about the effects on the size and structure of the spawning stocks or the genetics of species is largely missing.

In the life cycle of salmonids, some of the earlier stages still remain unrevealed. In boreal streams, where water temperature stays near 0 °C for several months, and occasionally even drops below it, physiology, survival, hatching and emergence period are still partly unknown (I), as well as the effects on them of harsh environmental conditions, like bottom ice covering redds or low discharge. In addition, the role of environmental and biological factors that determine survival of alevins in perhaps the most critical phase of the cycle, the emergence period, would need to be studied for egg stocking projects. In recent years, egg stocking has been used to restore trout populations in streams of the Finnish Lake District. In our incubation experiment (I), survival of embryos was high until hatching, but in egg stocking in the Kymijoki watercourse, the increase in parr density has varied from nothing to a moderate increase (Syrjänen et al. 2010b), and the reason for this is unknown. The secrets of the smolt phase, migration directions and destinations of wild smolts in lakes, have only just begun to be revealed in the Finnish Lake District (IV). The choice of parr to migrate or to stay in the stream and the existence of resident females should be studied at the individual and population level, to facilitate restoration of some migratory spawning stocks in the southern Finnish watercourses. However, there is only little information on a whole-lake scale about the level of fishing effort which the migratory stocks could endure and still recover (see Fig. 2).

In addition, the role of organic input from forests and bogs to small channels that affect channel morphology, retention capacity, prey availability, and fish and egg environment is still poorly understood in this country of very effective forest and bog utilization that has not historically paid much attention to its impacts on aquatic ecosystems. Another management issue that could be supported by research is an estimation of the sufficient level of salmonid populations that can maintain or increase pearl mussel (*Margaretifera margaretifera*) populations.

Acknowledgements

Right from the start it was “Mr. Running Water” himself, Timo Muotka, who got me hooked. He has since been the main supervisor throughout my research projects. In the beginning we worked together at the University of Jyväskylä, and then Timo moved to University of Oulu. During my studies, my interest towards the spotted fish living in running waters grew, and Tapani Valtonen organized for me to work with stream trout for my MSc thesis. Since Timo was already working in the same ecosystems albeit with a bit smaller animals, he help build my scientific thinking. However in our co-operation, I never understood the speciality in the game, where skaters skate after a tiny puck and crash into each others! I also express my gratitude to Juha Karjalainen, who guided me through fisheries issues and in finalising this thesis.

The other co-authors, Anssi Eloranta, Mikko Kiljunen, Kai Korsu, Pauliina Louhi, Riku Paavola and Pentti Valkeajärvi and the late Petri Kreivi did their parts extremely well, if not perfect, making the work easier for me. Timo Marjomäki sent me tens of fish articles during the years and gave new research ideas. Roger Jones improved the clarity of my thesis, by doing a complete linguistic check of the text.

Petri Heinimaa and other staff in Jyväskylä Game and Fisheries Research often offered a place for conversations and a cup of tea. With Konneveden kalatutkimus ry, I have had the opportunity to take part in interesting, small research projects throughout the past decade. I hope the 41-year-old society can continue its work for fishery studies. Sirkka Heinimaa at VesiSirkka Oy operated as an excellent consultant for these projects.

I have also had the pleasure to work in the field with the trout-oriented students: Kimmo, Pekka, Heli, Timo, Mikko, Mika, Matti × 2, Miika, Ilkka × 2, Olli × 2, Jouni, Markus, Antti and Ossi, many of which have graduated. Rod fishing and fish marking has given me an excellent counterbalance to office work, and I guess it was not too inconvenient for them either.

My previous and current office room mates Antti × 2, Kristian, Pete, Heikki, Jani, Jukka, Saija, Jussi, Heather and Santtu, as well as others in the unit, like Tapio, Kari, Heikki, Juhani, Jouni × 2 and Katja provided sufficiently varying conversations and rest during workdays. The technician masters, Juha, Tarmo, Hannu, Olli and Ahti repaired electrofishing gear dozens of times, and Harri kept my computer as healthy as possible. Tens of trainees helped in the field and laboratory during the years, and to my pleasant surprise, quite many of them decided to start to study biology in our university.

I have enjoyed and benefited from the meetings of NoWPaS, the European Workshop of Doctoral students on Salmo salar and Salmo trutta research, which has offered a very useful international network specializing in the issues that I work with.

YHTEENVETO (RÉSUMÉ IN FINNISH)

Luontaisten taimenkantojen ekologia, kalastus ja hoito pohjoisilla sisävesillä

Tämän tutkimustyön tarkoituksena oli tutkia taimenen (*Salmo trutta* L.) alkio- (I) ja jokipoikasvaiheen (II) ekologiaa pohjoisen havumetsävyöhykkeen joissa, selvittää virtavesikunnostusten vaikutuksia uomiin ja niiden eliöstöön (III) sekä kuvailla villien taimenkantojen tilaa ja hoitotoimien onnistumista Kymijoen vesistössä (IV).

Taimenen alkioiden kasvua ja säilyvyyttä sekä poikasten kuoriutumis- ja sorastanousujakson ajankohtaa tutkittiin mädinhaudontakokeilla kahdessa Päijänteeseen laskevassa joessa, Arvajanjoessa ja Rutajoessa. Alkio- ja sorastanousuvaiheen ekologia on kenties heikoimmin tunnettu vaihe lohikalojen elinkierrossa, mutta säilyvyys sorastanousuvaiheessa saattaa vaikuttaa voimakkaasti vuosiluokan runsauteen. Haudontakokeessa käytettiin muoviverkosta koottuja sylintereitä, ja koe tehtiin molemmissa joissa sekä järviluusuassa että järvestä kauempana olevassa koskessa. Suuren järven luusuassa jokiveden lämpötila pysyi läpi talven alimmillaan noin 1 °C:ssa, kun muilla kolmella koskella lämpötila putosi useiden viikkojen ajaksi 0,0-0,2 °C:een. Alkiot kasvoivat talvella suuren järven luusuassa lämpimämmän veden ansiosta selvästi nopeammin kuin pienen järven luusuassa tai alemmissa koskissa, mutta kasvuero hävisi keväällä, ja sorastanousun ajankohta arvioitiin kaikissa kohteissa lähes samaksi, touko-kesäkuun vaihteeksi. Mätimunien ja alkioiden säilyvyys hedelmöityksestä kuoriutumiseen asti oli korkeaa (83-98 %) kaikissa kohteissa.

Toinen keskeinen tavoite oli selvittää taimenen jokipoikasten ravinnonkäyttöä, -saatavuutta ja -valintaa alkukesällä ja alkusyksyllä 25 suomalaisessa joessa, jotka jaoteltiin kolmeen kokoluokkaan: pieni, keskikokoinen ja suuri. Taimenet pyydettiin sähkökalastamalla, ja ravintonäytteet otettiin nukutetuilta kaloilta vatsahuuhtelulla. Taimen käytti taksonomis-morfologisia ravintoeläinryhmiä siinä suhteessa kuin niitä oli saatavilla pohjaan kiinnittyneinä sekä ajeessa eikä yleisesti erikoistunut selvästi mihinkään ryhmään. Taimen oli kaikkiruokainen sekä suuren ravintoeläinmäärän tuottavissa suurissa luusuajoissa että vähemmän ravintoa tarjoavissa pienissä metsäpuroissa. Runsain saalisryhmä koko aineistossa oli mäkärän toukat. Pienissä joissa taimen käytti eniten mäkärän ja koskikorentojen toukkia sekä maaeläimiä, keskikokoisissa joissa kopallisten vesiperhosten, suodattajavesiperhosten, päivänkorentojen ja koskikorentojen toukkia sekä suurissa joissa kopallisten vesiperhosten, suodattajavesiperhosten ja mäkärän toukkia. Alkukesällä taimen valikoi suhteessa ravintoryhmien tarjontaan koskikorentoja, aikuisia vesihyönteisiä ja suodattajavesiperhosia sekä alkusyksyllä kopallisia vesiperhosia. Selvitin työssä myös kirjallisuushaun avulla maalta peräisin olevan ravinnon merkitystä lohikalojen jokipoikasille kesäaikana. Rantakasvillisuuden tila vaikuttaa veteen putoavien maaselkärangattomien määrään, joten rantakasvillisuuden hyödyntäminen ja hoito vaikuttaa jokipoikasten ravintoryhmien saatavuuteen. Käytin tässä osiossa julkaistuja tietoja 41 tiedeartikkelista sekä omaa aineistoani, joten havaintopisteitä kertyi 122. Maaeläinten osuus jokipoikasten ravinnossa oli keskimäärin 17 %. Osuus oli pienin, 12 %, pienimmällä kalakokoluokalla (< 80 mm) ja suurin, 25 %, suurimmalla kokoluokalla (≥ 150 mm). Myös kalasuvut erosivat toisistaan. Tyynenmeren lohet (*Oncorhynchus*) käyttivät ravinnostaan maaeläimiä keskimäärin 27 %, nieriät (*Salvelinus*) 23 % sekä taimen ja lohi (*Salmo*) 9 %. Maaeläinten osuus vaihteli myös rantakasvillisuusluokan mukaan: osuus oli suurin, 30 %, lehtimetsärantaisilla joilla ja pienin, 11 %, havumetsärantaisilla sekä avoimilla ja pajurantaisilla joilla.

Virtavesiuomien yleisesti käytetyn hoitomenetelmän, koskikunnostuksen, vaikutuksia ja onnistumista selvitin yleiskatsauksella suomalaisten koskikunnostustutkimusten tuloksiin. Käytin työssä myös omaa aineistoani Päijänteen valuma-alueelta. Työ sisälsi tutkimusta uoman morfologiasta, pohjaeläinyhteisöstä, taimenen poikastiheydestä sekä uoman orgaanisen aineksen pidätyskyvystä. Tutkimusmenetelmät käsittivät veden syvyyden, virrannopeuden, pohjan raekoon ja sammalpeittävyyden mittausta, puolipallojen käyttöä virranpaineen laskemisessa, virtaustyyppien osuuksien arviointia pinta-alamittauksella, pohjaeläinnäytteenottoa, sähkökoekalastusta poikasinventoinneissa sekä keinolehtikellutuskokeita. Uoman pohjaprofiili muuttui kunnostuksessa karkeammaksi, veden syvyysvaihtelu ja pohjan raekoon vaihtelu kasvoivat, virrannopeus ja sammalpeittävyys pienenivät ja virranpaine väheni. Suvantojen (pool) osuus pysyi kunnostuksessa ennallaan joen pinta-alasta, mutta huomattava osuus pintakivettömistä koskista (run) muuttui kivisiksi koskiksi tai saheiksi (riffle). Pohjaeläinyhteisöjen lajistorakenne muuttui kohti luonnontilaisten uomien rakennetta, mutta ei saavuttanut sitä. Taimenen poikastiheys ei muuttunut kunnostuksen seurauksena. Orgaanisen aineksen pidätyskyky, jota tutkittiin keinolehtikellutuskokeella, kasvoi, mutta ei saavuttanut luonnontilaisen uoman tasoa. Uomat levenivät kunnostuksessa hieman, 10-20 %, mutta ne eivät saavuttaneet alkuperäistä leveyttänsä.

Viimeinen tavoite oli arvioida vaeltavien villien järvitaimenkantojen tilaa Kymijoen vesistössä verrattuna Paatsjoen (Inarinjärven) ja Koutajoen vesistöön sekä arvioida kantojen katoamisen syitä ja mahdollisia elvytystoimia. Taustoitin eteläisten vaeltavien kantojen tilaa viimeisen sadan vuoden ajalta kotimaisten raporttien avulla. Kantojen nykytilaa selvitin kutupesälaskennalla, poikasinventoinnilla sekä jokipoikasten merkinnällä. Kokosin myös tietoa verkkopyyntiponnistuksesta sekä suurten taimenyksilöiden osuudesta järvikalastuksessa. Kymijoen vesistössä neljällä suurjärvellä verkkopyyntiponnistus verkkovuorokausina oli 5-12 verkkovrk ha^{-1} $vuosi^{-1}$, ja kokonaispituudeltaan vähintään 60 cm mittaisten yksilöiden osuus taimensaaliissa oli alhainen (4-8 %). Kalat pyydetään todennäköisesti pääosin pois ennen kuin ne ehtivät saavuttaa 60 cm pituuden. Kymijoen vesistön virtavesissä kutupesät olivat pieniä, (keskipituus 1,5 m, keskiala 1 m^2). Suuria pesiä (pituus vähintään 2,5 m, ala vähintään 2 m^2) löydettiin hyvin vähän. Poikastiheys oli keskimäärin matala tai kohtalainen (1-14 yksilöä 100 m^{-2}). Paatsjoen ja Koutajoen suurjärvillä, Inarinjärvellä ja Pääjärvellä, verkkopyyntiponnistus oli 3 verkkovrk ha^{-1} $vuosi^{-1}$ tai pienempi ja suurten yksilöiden osuus taimensaaliissa oli 13-25 %. Inarinjärven ja Pääjärven virtavesillä kutupesät olivat suurempia (keskipituus 2,5-3,3 m ja keskiala 2-4 m^2) eikä pieniä (< 1,5 m) pesiä esiintynyt. Poikastiheys oli yleensä kohtalainen tai korkea, (5-30 yksilöä 100 m^{-2}). Tulosten perusteella vaikuttaa ilmeiseltä, että korkea kalastuskuolevuus estää villin järvitaimenen elinkierron eteläisillä sisävesillämme.

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