

Saija Koljonen

ECOLOGICAL IMPACTS OF IN-STREAM RESTORATION IN SALMONID RIVERS

*THE ROLE OF ENHANCED STRUCTURAL
COMPLEXITY*

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**ECOLOGICAL IMPACTS OF
IN-STREAM RESTORATION
IN SALMONID RIVERS**

The role of enhanced structural complexity

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Abstract

Despite the great amount of in-stream restorations conducted in the past decades there is still a disturbing lack of knowledge about the outcome of these measures. The overall goal of this study was to assess the effect of enhanced streambed heterogeneity on the ecology of stream salmonids and stream retention efficiency. Substratum heterogeneity is often considered as one of the most important limiting factors for organisms living in running waters.

Winter ecology of rivers has not been broadly studied regardless of the general belief that wintertime conditions strongly influence the survival and population size of stream salmonids. In an experimental study, the paucity of wintertime habitat in simplified channels caused temporary mass loss in age-0 trout. In late spring, channelized stream trout performed catch-up growth with potentially negative effects on long-term fitness. A management implication of this study is that increasing cover availability by in-stream restoration structures may enhance the long term success of juvenile salmonids although the short term effects were minor.

Densities of salmon parr in the River Kiiminkijoki showed no response to streambed restoration. Suitable habitat area for salmon parr increased after restoration under summer conditions. However, restoration-induced benefits to winter habitats were marginal, with one study reach indicating even negative values. Most of the areas with good habitat values were located along river margins, indicating that restoration measures had only limited impact on the mid-sections of the river channel.

Dredging of small streams may have caused depletion of allochthonous organic matter due to the reduction of retentive structures. In a leaf release experiment, moss cover enhanced retentiveness as well as did various restoration structures (boulders, large wood). Only a very high amount of wood clearly enhanced retention capacity. This underlines the importance of wood as an effective retention structure in headwater streams.

This study indicates that habitat complexity as such may be less important than life-stage specific habitat requirements of fish (e.g. cover for overwintering salmonids). Importantly, restoration may only be successful if the measures used target the limiting factor(s) of the ecosystem or the species; for salmonids, habitat complexity does not seem to be this factor.

Keywords: brown trout, habitat complexity, hydraulic modeling, rehabilitation, restoration, river, salmon, stream, winter ecology

Koljonen, Saija, Koskikunnostusten ekologiset vaikutukset. Elinympäristön rakenteellisen monimuotoisuuden merkitys

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Tiivistelmä

Uiton jälkeisten kunnostustoimenpiteiden määrä Suomessa on ollut huomattava, mutta vaikutusten arviointi, pelkästään kalastonkin kannalta, on jäänyt vähäiselle huomiolle. Tässä työssä selvitettiin kunnostusten merkitystä lohen ja taimenen poikasvaiheille, huomioiden etenkin pohjan rakenteellisen monimuotoisuuden vaikutus. Työssä selvitettiin myös kunnostusten vaikutuksia lehtikarikkeen pidätyskykyyn, joka on erityisesti latvapurojen ekosysteemien tärkeimpiä perustoimintoja.

Lohikalojen talviekologinen tutkimus on viime aikoihin saakka ollut vähäistä, vaikka talviolosuhteiden uskotaan rajoittavan pohjoisten virtavesien eliöstön elinmahdollisuuksia. Kokeellisessa työssä rännimäisissä uomissa talvehtiminen aiheutti taimenenpoikasille tilapäisen painon alenemisen ja nopean kompensatiokasvun loppukevällä. Kompensatiokasvu voi vaikuttaa negatiivisesti koko kalan eliniän, joten kunnostusten tuoma hyöty sopivien suojapaikkojen lisääntymisenä voi edesauttaa lohikalojen pitkäaikaista menestymistä.

Kiiminkijoella lohenoikasten tiheydet eivät muuttuneet kunnostuksen myötä ja vuosien välinen vaihtelu oli kuuden vuoden seurantajaksolla huomattavan suurta. Elinympäristömallinnuksen perusteella soveltuvan elinympäristön lisäys ei ollut merkittävää, koska etenkin talviaikaisen alueiden puute jäi huomattavaksi. Suurin osa soveltuvasta elinympäristöstä sijaitsee joen reuna-alueilla, joten kunnostusvaikutus joen keskiosaan jäi odotettua pienemmäksi.

Uittoperkaus on voinut johtaa latvesien ekosysteemien köyhtymiseen maalta tulevan orgaanisen aineksen pidättymiskyvyn vähentyessä. Kokeellisen työn perusteella kuitenkin nykypäivän tilanne vuosikymmeniä uiton loppumisen jälkeen osoittautui lähes yhtä pidättäväksi kuin nykyisin käytetyt kunnostusrakenteet (kivi tai puu). Kunnostusrakenteeseen tulisi lisätä huomattava määrä puuta, jotta lehtikarike pidättyisi korkeallakin virtaamatasolla.

Tulosten perusteella elinympäristöjen muuttaminen monimuotoisemmiksi ei takaa kunnostustoimien onnistumista, sillä etenkin kalapopulaatioita rajoittavat yleensä useat tekijät. Jos kuitenkin elinympäristö on populaatiota rajoittava resurssi ja sitä pystytään lisäämään (kuten talviaikaiset suojapaikat), voidaan kunnostuksella saada näkyviä tuloksia. On ilmeistä, että kunnostustoimien tulisi olla nykyistä kattavampia ja paremmin suunnattuja rajoittaviin tekijöihin, jotta tulokset näkyisivät.

Asiasanat: elinympäristö, habitaattimallinnus, joki, kunnostus, lohi, lohikalat, taimen, talviekologia, virtavesi

“Science, my lad, is made up of mistakes, but they are mistakes which it is useful to make, because they lead little by little to the truth.”

Jules Verne (A Journey to the Center of the Earth)

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I started my career as a fish biologist at the age of three by studying the gut contents of *Salmo salar* L. caught from the Lake Saimaa, where our family spent its summers. My parents have always encouraged and supported me to follow my path. I extend my warmest thanks to my childhood family, for giving me the home that let me become me.

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List of original papers

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

- I Huusko A, Greenberg L, Stickler M, Linnansaari T, Nykänen M, Vehanen T, Koljonen S, Louhi P & Alfredsen K (2007) Life in the ice lane: the winter ecology of stream salmonids. *River Research and Applications* 23: 469–491.
- II Koljonen S, Huusko A, Mäki-Petäys A, Mykrä H & Muotka T (2010) Body mass and growth of overwintering brown trout in relation to stream habitat complexity. *River Research and Applications*. In press.
- III Koljonen S, Huusko A, Mäki-Petäys A, Louhi P & Muotka T (2011) Assessing habitat suitability for juvenile Atlantic salmon in relation to in-stream restoration and discharge variability. Manuscript.
- IV Koljonen S, Louhi P, Huusko A, Mäki-Petäys A & Muotka T (2011) Quantifying the roles of in-stream habitat structure and discharge to leaf retention: implications for stream restoration. Manuscript.

Table of contents

Abstract	
Tiivistelmä	
Acknowledgements	9
List of original papers	11
Table of contents	13
1 Introduction	15
2 Aims of the thesis	21
3 Material and methods	23
3.1 Literature survey on winter ecology of stream salmonids (I)	23
3.2 Experimental protocol (II, IV)	23
3.2.1 Body mass and growth of overwintering brown trout (II).....	23
3.2.2 Leaf litter retention capacity (IV).....	24
3.3 River Kiiminkijoki (III)	25
3.3.1 Study area	25
3.3.2 Physical habitat modeling.....	26
3.3.3 Monitoring densities of young Atlantic salmon.....	28
4 Results and discussion	29
4.1 Overwintering of brown trout – emphasis on habitat structure (I,II).....	29
4.2 Evaluating the effect of in-stream restoration on salmon by habitat modeling (III)	31
4.3 Responses of litter retention to in-stream restoration (IV).....	32
5 Pitfalls and scenarios of habitat models	33
6 Restoration success: from assessment to management implications	35
References	39
Original publications	47

1 Introduction

Human-induced changes are causing the next mass extinction through, for example, habitat loss (Barnosky *et al.* 2011), and freshwaters, particularly rivers and streams are one of the most threatened ecosystems of the earth (e.g. Tockner 2009, Dudgeon 2010, Vörösmarty *et al.* 2010). To reverse this negative trend, a massive amount of diverse restoration projects has been initiated in several ecosystems, and the 21st century has been called “the era of restoration in ecology” (Wilson 1992).

In Finland alone, there have been hundreds of stream restoration projects during the past few decades. It has been estimated that the state uses 1.8 million euros yearly for river restorations aiming to enhance the ecological state of an ecosystem (Finnish Environment Institute 2010). In the U.S., the amount used for 37 000 restoration projects exceeded 9 billion USD (Bernhardt *et al.* 2005). A major problem remains however: we do not know whether investment in restoration has been worthwhile. Assessment and monitoring of restoration outcomes have been largely ignored, yet both habitat monitoring and species inventories are essential to evaluating the success of investments (Vörösmarty *et al.* 2010). Considerable funds worldwide are spent to restore the in-stream habitat, but few projects are being monitored, particularly over long (>5 years) time periods (Enterkin *et al.* 2008). Monitoring has been the obvious black spot of the field and seems to remain that way (see e.g. Eloranta 2004, Palmer *et al.* 2007, Roni *et al.* 2008, Stewart *et al.* 2009, Louhi 2010, Whiteway *et al.* 2010).

The history of human impact on running waters extends far beyond the written history, albeit the most extensive changes have taken place in modern times. Hydropower production, irrigation and transportation, for example, have had a direct impact on streams. In vast areas of the boreal region, numerous streams have been dredged to facilitate water transport of timber. In Finland, almost all the streams in forested areas were used for timber floating, at least for a short period of time. A total of 40 000 km of water courses (including rivers and lakes) were evaluated as suitable for floating (Lamassaari 1990). Dredged river channels exceeded 13 000 km by the 1950's and dredging continued until the 1970's (Lamassaari 1990), encompassing well above 20 000 km of rivers.

In-stream restoration planning and implementation have been built on the hypothesis that increasing habitat heterogeneity enhances system recovery (Osborne *et al.* 1993, Gore *et al.* 1995, Stanford *et al.* 1996, Palmer *et al.* 1997). Indeed, loss of habitat complexity has been considered a serious threat to the

persistence of natural communities as it influences ecological interactions and community dynamics (Pickett *et al.* 1996, Dobson *et al.* 1997, Willis *et al.* 2005). Recently, however, Gibb & Parr (2010) questioned our understanding of the global rules determining the effects of habitat complexity and underlined the interplay between complexity, scale and other factors. Chapman and Knudsen (1980) prioritized the loss of habitat complexity as the main factor for salmon and trout population losses. In simplified streams, boulder placement has resulted in an increase of fish abundance (Näslund 1989, Hvidsten & Johnson 1992, Roni *et al.* 2006, Dollinsk *et al.* 2007, Venter *et al.* 2008). Also on a larger scale, habitat complexity has been found to increase fish abundance (Willis *et al.* 2005, Eitzman *et al.* 2010), although opposite results of no response to structural complexity have also been published (Lepori *et al.* 2005, Thompson 2006, Dollinsk *et al.* 2007, Vehanen *et al.* 2010). In salmonid studies, mixing of habitat complexity and shelter availability, both of which may be increased by boulder placement, may give unjust credit to complexity. Shelter availability was identified by Finstad *et al.* (2007) as a key habitat factor for salmonids, although depth may also provide shelter for fish (Gibson & Erkinaro 2009). Lack of suitable spawning habitat has often been raised as one of the reasons for the weak response by salmonids to management actions. Indeed, Palm *et al.* (2007) demonstrated that adding large amounts of spawning gravel enhanced densities of age-0 brown trout in Swedish streams much more than did increased habitat complexity per se (see also Pedersen *et al.* 2009). Studies on running water communities have revealed that the link between habitat heterogeneity and biotic diversity is questionable at best (Brooks *et al.* 2002, Muotka *et al.* 2002, Lepori *et al.* 2005, Miller *et al.* 2010, Louhi *et al.* 2011). These results strongly suggest that habitat complexity, as such, does not lead to system restoration or alternatively, complexity has been studied on an inappropriate scale.

When Fennoscandian streams were channelized, only major flow obstacles were removed from the streambed and the loss of habitat heterogeneity was only partial (Nilsson *et al.* 2005). In some rivers, however, boulders were removed with explosives or lifted to the banks, meanders were straightened and side-channels blocked (Yrjänä 1998, Eloranta 2004). The loss of natural-state riffles and rapids was thus extensive. It seems, however, that the loss of heterogeneity has not been detrimental to macroinvertebrates (Lepori *et al.* 2005, Louhi *et al.* 2011). Recently, Miller *et al.* (2010) reported in a meta-analysis that restoration enhances benthic macroinvertebrate species richness, but not density. Yet macroinvertebrates are a key resource to higher trophic levels, e.g. fish. It seems

that macroinvertebrate indicators are insensitive to streambed rehabilitation (Matthews *et al.* 2010), or their community structure is controlled by larger scale factors (Malmqvist & Hoffsen 2000, Townsend *et al.* 2003, Suren & McMurtrie 2005). Because of the high natural variability of macroinvertebrate communities, many studies have urged research and monitoring to focus on ecosystem base functions, e.g. retention capacity, decomposition, or primary productivity (Brooks *et al.* 2002, Wohl *et al.* 2005).

Bryophytes (e.g. *Fontinalis* ssp.) have a key role in the trophic dynamics of many woodland streams (Suren & Winterbourn 1992), and they often suffer a drastic loss if restoration is conducted with an excavator (Muotka & Laasonen 2002). The role of mosses to ecosystem functioning relates to their high retention capacity and they also provide suitable feeding grounds for benthic macroinvertebrates, particularly their juvenile stages. Recovery time for aquatic mosses is long and apparently site specific, as even after 30 years from restoration mosses had not emerged in one monitored site (Huhtala 2008) while the moss biomass had recovered almost fully within 6–8 years in some sites (Muotka *et al.* 2002). Bed material may remain unstable for years or even decades after restoration which can further complicate recolonization by mosses. Thus bryophytes should be left at least partially untouched during restoration works to serve as a source for expansion (Korsu 2004, Louhi *et al.* 2011).

As benthic invertebrate communities in channelized streams 20–30 years after the cessation of timber floating do not differ appreciably from natural reference streams, the need for restorations (at least for benthic diversity) has been questioned (Louhi *et al.* 2011). Nevertheless, the loss of salmonid populations during the same time period has been drastic. There has been a more than 90% decline in the Baltic salmon populations within a few decades (Ackefors *et al.* 1991). However, the post-channelization period was also the time of extensive land use change (forestry, ditching, peat mining, intensive farming), with considerable changes to water bodies (hydropower production, intensive fisheries, eutrophication). These changes caused habitat loss, decreased water quality, altered flow regimes and possibly reduced reproductive output of salmon populations. The loss of Baltic salmon was in fact mainly caused by damming and river regulation (Ackefors *et al.* 1991). Salmonid population reduction caused by dredging and deteriorated habitats has not been quantified, although loss of suitable spawning and juvenile habitats has been observed (Jutila *et al.* 1998, Scruton *et al.* 1998).

Finnish in-stream rehabilitation projects are usually mainly or entirely focused on salmonids of economical interest (salmon *Salmo salar* L. and brown trout *Salmo trutta* L.). During the past decades, increased salmonid density has been the key factor that managers have been interested in when performing restorations. Ecosystem level re-establishment projects aiming to restore biodiversity have emerged over the last decade, possibly encouraged by the theory of ecosystem resilience in species rich systems (Palmer *et al.* 2007). Broad ecological standards for river restorations have been issued, emphasizing the need for setting a 'guiding image' for each project and including long-term monitoring (Palmer *et al.* 2005, Giller 2005, Wohl *et al.* 2005).

The ultimate goal of salmonid-centred in-stream restorations is the restoration of the natural life cycle of the target species – a highly complicated assignment. Lack of in-stream structures may play a key role in only a limited number of projects while other factors like unrestricted migration, overfishing and poor water quality are the general bottlenecks for salmonid populations. In-stream rehabilitation may be a key factor only if habitat is limiting the population at some point of the life cycle. This might be the lack of suitable spawning, feeding, resting or overwintering habitat. As restoration success in an ecological perspective is clearly site specific, it is likely impossible to identify a universal restoration measure that would be equally effective everywhere. Negishi and Richardson (2003) stress that restoration involving in-stream structures should be planned in the context of large-scale natural processes, taking into account the geomorphic characteristics of stream channels.

Winter has been thus far little studied in boreal streams, due probably to harsh environmental conditions restricting the performance of field studies. However, juvenile salmonids are well adapted to winter conditions and a clear bottleneck for overwinter survival has not been identified (Huusko *et al.* 2007). Nevertheless, habitat characteristics, particularly the amount of shelter (Finstad *et al.* 2007), may have a positive impact on long-term survival, indicating the importance of suitable habitat during the winter.

Evidence on the effectiveness of restoration projects is equivocal. In the U.S., the history of installing in-stream structures to improve fish stocks leads back to the 1880's (Van Cleef 1885 *in* Thompson & Stull 2002). Despite the long history and widely accepted methodology, Thompson's review (2006) indicated that the traditional use of in-stream structures for channel restoration does not ensure demonstrable benefits for fish communities, and their ability to increase fish populations should not be uncritically assumed. Two meta-analysis about the

effectiveness of habitat heterogeneity and in-stream structures in salmonid rehabilitation projects have been recently published (Stewart *et al.* 2009, Whiteway *et al.* 2010). One finding in Stewart *et al.* (2009) was that in-stream devices are less effective for increasing salmonid population size in large compared with small streams. Whiteway *et al.* (2010) found a significant increase in salmonid density and biomass following the installation of structures although large differences between species were observed, such that anadromous and juvenile salmonids tended to benefit least. The duration of monitoring averaged three years which may be too short to determine the effectiveness of a project. Kondolf and Micheli (1995) recommended at least 10 years post-restoration monitoring, a much longer period than is typical for most monitoring programs.

2 Aims of the thesis

Habitat heterogeneity is often considered as one of the key regulators of organisms and communities living in running waters. The general aim of this thesis was to assess the ecological impacts of streambed heterogeneity and its effects on in-stream restoration success in salmonid rivers. The thesis concentrates on salmon and trout (I–III) but it also addresses one of the basic processes of the boreal headwater ecosystem, retention capacity of a stream to organic matter inputs (IV). Wintertime and overwintering issues constitute one part of this work, aiming to define the effect of structural heterogeneity on overwintering success (I–II). A field test of restoration success for juvenile Atlantic salmon was made in the River Kiiminkijoki where changes to river bed structure and salmon populations were followed before and after restoration (III). Data allowed the use of hydraulic habitat modeling as a tool for assessing changes in salmon habitat, thus providing numerical information about restoration success. Organic matter retention capacity is a basis for a functional stream ecosystem; hence various restoration structures were tested for their efficiency in leaf retention (IV).

3 Material and methods

3.1 Literature survey on winter ecology of stream salmonids (I)

Despite the general belief that conditions in winter strongly influence survival and population size of fish, the overwintering ecology of salmonids, and other fishes as well, has not been extensively studied (Cunjak 1996, Reynolds 1997). The focus of the review was set to behaviour and ecology of riverine stages of overwintering salmonids. However, because of the close linkage between physical habitat and fish ecology, both physical and biological elements were discussed. The main objective was to summarize the latest information about the survival, habitat use, movement and biotic interactions of riverine stages of overwintering salmonids and assess its relation to the prevailing physical conditions in rivers and streams during winter. Such information should be of use to both ecologists and resource managers interested in identifying fish production bottlenecks and effective management of boreal streams. Not surprisingly, the conducted studies with winter-related issues in lotic fish research during the recent decades have provided much new information about overwintering fish.

3.2 Experimental protocol (II, IV)

The experiments for studies II and IV were conducted in six parallel semi-natural stream channels in the Finnish Game and Fisheries Research Institute's research station in Paltamo, northern Finland (64°N, 27°E). The channels are 25.5 m long and 1.5 m wide. The channel walls are made of concrete, but the stream bed is constructed of natural materials, such as gravel, cobbles and boulders. For both studies, a 10–15 cm layer of coarse gravel/pebble (20–35 mm in diameter) was placed onto the channel bed, which had a gradient of 0.3%.

3.2.1 *Body mass and growth of overwintering brown trout (II)*

Three randomly selected channels were constructed to mimic simplified (channelised) streams, whereas three other channels mimicked natural (or restored) streams with heterogeneous bed structure. A similar amount of cobble-to-boulder sized stones (>128 mm in diameter) were added to each channel, but with differing spatial arrangement. In the restored streams, stones were placed across

the channel bed, often clustered perpendicular to the flow, resembling weirs and deflectors of natural streams. Stones in the channelised streams were placed along channel margins, leaving the middle section open. Thus the spatial configuration of habitat suitability for age-0 brown trout differed strongly among the channel types.

We introduced 40 age-0 (total length 94 ± 1.42 mm, mass 8.5 ± 0.41 g) and 10 age-1 (length 180 ± 6.42 mm, mass 58.5 ± 6.51 g) (means ± 1 SE) brown trout to each channel. Before introduction, fish were individually PIT-tagged. During the study, fish were sampled using one-pass fishing trials, on 10 January (mid winter), 2 April (late winter) and 7 May (early spring). Each fish captured was identified, measured, and released back to the channel at the position of capture. Sixteen fish of both age classes were captured on all sampling occasions in both channel types. We used repeated measures ANOVA (rmAnova) with Greenhouse-Geisser corrected degrees of freedom to test for the effects of treatment on the growth rate of overwintering trout. We calculated specific growth rates ($SGR = (M_2 - M_1) / (t_2 - t_1)$ g d⁻¹, where M_1 and M_2 are the initial sizes at times t_1 and t_2) individually for each fish between each pair of successive dates. We also used nested rmAnova to examine whether fish in the two treatments (channelised vs. restored) were differentially positioned in relation to distance from (i) stream edge and (ii) upstream end of a stream.

3.2.2 Leaf litter retention capacity (IV)

This experiment included two factors, substratum heterogeneity (five levels) and stream flow (three levels), with five replicates for each treatment combination. The substratum-treatment levels six were selected to reflect a series of increasing bed complexity: (i) dredged channels, (ii) dredged channels + moss transplants, (iii) stony enhancement structures, (iv) stones + moss, (v) wood, and (vi) extra amount of wood (3 x the amount of wood in v; conducted only at the highest flow level). The flow treatment had three levels: low (0.009 m³ s⁻¹), intermediate (0.055 m³ s⁻¹), and high (0.120 m³ s⁻¹). All channels had three fast flowing parts (runs or riffles) where the restoration structures were constructed. Two upper runs followed deeper and slower flowing spools and the third run ended to a shallow ending slide and a mesh.

The dredged channel was a simple U-shaped stream with only gravel on the bottom. The second treatment was otherwise similar but with moss transplants (*Fontinalis* spp. collected from two nearby streams) to indicate situation years or

even decades after dredging). The moss covered approximately 45% of the fast flowing area of a channel which is concordant with observations from natural stream sites (Muotka & Laasonen 2002). Treatments with added wood contained three short sections with small logs (mean diameter: 12 cm), the total amount of wood equalling $50 \text{ m}^3 \text{ ha}^{-1}$. In the stone restoration treatment, the restoration structures consisted of a constant number of small stones (40 stones, mean diameter 14 cm), the quantity of the added stone material equalling to $142 \text{ m}^3 \text{ ha}^{-1}$ for a riffle. The stone-and-moss restoration was equal to plain stone restoration, with mosses added at about 45% cover to the run sections. The treatment with extra amount of wood contained approximately four times more wood than the treatment (v), thus equalling $208 \text{ m}^3 \text{ ha}^{-1}$ of woody material. The aim of this treatment was to mimic naturally fallen trees with branches extending across the water surface. After each trial, all restoration structures were removed and the treatments were re-allocated randomly to each channel. Each leaf retention float compounded of two hundred plastic leaves, sized 5 x 6 cm, which were let to flow and settle for one hour. We used different colours of plastic leaves to represent different flow regimes because of the fact that it was not always possible to detect all the leaves from a float without dismounting the constructions. We used artificial leaves because the previous experiments showed that natural leaves were hard to relocate after the float and on the other hand plastic leaves were earlier used successfully (Muotka & Laasonen 2002) and are known to behave much like freshly fallen natural leaves entering the stream (Speaker *et al.* 1988).

3.3 River Kiiminkijoki (III)

3.3.1 Study area

The study was conducted in the River Kiiminkijoki, a 170-km long, free-flowing humic river in northern Finland with a mean annual flow (MQ) of $44 \text{ m}^3 \text{ s}^{-1}$. One third of the peatland-dominated catchment area of the river (total of 3845 km^2) is ditched for forestry purposes. Extensive draining of the catchment has resulted in relatively low pH (range 5–7), and high concentrations of humic substances and nutrients.

Kiiminkijoki was dredged for timber floating by the early 1950s when most of the rapids were channelized, i.e. at least the mid-channel section of the rapids was cleared of all major floating obstacles. Some rapids, however, remained

nearly pristine. Timber floating ceased by the end of the 1960s and the first remedial actions were taken in 1984, aiming at removing the most visible signs of timber floating modifications without any detailed consideration of ecological aspects. A more versatile restoration attempt in 2003 aimed to enhance fish habitat availability, with the primary goal of re-establishing naturally-spawning populations of Atlantic salmon. Loss of natural heterogeneity due to dredging and increased amount of humic substances, together with over-fishing, had demolished the native salmon population of river Kiiminkijoki by the end of the 1970s.

River Kiiminkijoki was restored in summer 2003. Enhancing habitat availability for different life stages of salmonid fish is the shared objective of most restoration attempts in Finland. Typically this involves modification of hydraulic conditions to enhance local habitat heterogeneity, with the intent of providing better habitat for salmonid fish (Huusko & Yrjänä 1997, Yrjänä 2003). This is achieved by re-arranging the stream bottom using boulders that were removed from the channel and placed along stream margins during channelization. This material is used to construct boulder ridges, flow deflectors and other in-stream enhancement structures placed across the stream channel. These measures are known to be very effective in enhancing the structural complexity of in-stream habitat at multiple spatial scales (Muotka & Syrjänen 2007).

3.3.2 Physical habitat modeling

Hydrological and geomorphological factors are considered to be fundamental in stream ecology, affecting species distribution and abundance (Bovee 1986, Heggenes 1996). In the past few decades, many studies have been completed to specify the most important physical factors for various species. Several studies with salmonids have led to the conclusion that water velocity, depth and substrate (in unison with cover availability) are essential factors for salmonid habitat selection (Heggenes 1996). Hydraulic habitat models were developed to get quantified evidence of the suitability of the habitat for a given species, particularly in relation to human induced changes.

Three channelized reaches (60 m to 115 m long; 37 m to 70 m wide) in the River Kiiminkijoki were selected to assess in-stream restoration effects and, correspondingly, three unmodified reaches (60 m to 110 m long; 30 m to 80 m wide) were selected for reference. Within each study reach, geographically-referenced river bed topography was quantified before and after restoration with a

total-station. To specify local bottom roughness for hydraulic modelling, we also estimated dominant substrate size at each measurement point using a modified Wentworth scale (see e.g. Vehanen *et al.* 2010).

The field data were entered into River2D (Steffler & Blackburn 2002) to create a hydraulic model for each reach. River2D is a depth-averaged finite-element procedure developed for hydraulic modelling of natural streams. First, the site-specific georeferenced topographic data were entered into River2D to construct and fine-tune a terrain model over each study reach, both before and after restoration (or two trials of field measurements for the reference reaches). Then, a two-dimensional hydraulic model available in River2D was used to calculate local water depths and velocities over the study reach at six flow conditions: 2, 10, 20, 40, 60 and 100 m³ s⁻¹. Each flow model was calibrated to match the field-measured boundary conditions (modelled discharge and subsequent water level) at each study reach. Water depths and mean water column velocities at flow levels other than the modelled ones were determined by linear interpolation from the six calibrated flow models.

To assess restoration success and its annual variability, we selected a 10-year period (1997–2006) of discharges in the river Kiiminkijoki (Environmental Information System HERTTA, Finnish Environment Institute), and estimated the weighted usable areas (WUA values) for different life stages of Atlantic salmon using average weekly discharges under both dredged and restored stream conditions. The weekly mean discharge and corresponding WUA were calculated from the end of the intragravel stage for the next 16 months, thus including the period of the life of young Atlantic salmon that is considered most critical for survival. We used the summer habitat preference criteria (HPC) of young-of-the-year Atlantic salmon from early June to late October (‘first-summer life stage’), thereafter the winter HPCs until the onset of spring flood in May (‘first-winter life stage’). From early June to late October we applied the HPCs of age-1 Atlantic salmon (‘second-summer life stage’). We did not perform modeling for the peak flows during the spring flood as these were almost ten times higher than the mean annual flow and published information on the HPCs of juvenile salmon under such conditions is unavailable.

The change in the WUAs by different life history stages of salmon during the ten water years was tested using linear mixed-effect model (LME), which allows the incorporation of fixed factors and random effects that control for correlation in data arising from grouped observations (Pinheiro & Bates, 2000).

3.3.3 Monitoring densities of young Atlantic salmon

As the Atlantic salmon population in the River Kiiminkijoki was sparse, each study reach was stocked with age-0 Atlantic salmon at equal density (10 fish 100 m⁻²) every September, starting from year 2000. From 2001 to 2006, Atlantic salmon densities in the study reaches were estimated by three-pass electrofishing trials conducted in August each year. In each study reach, three sampling sites (area 60–100 m²) were fished, age-1 Atlantic salmon density was estimated for each site by the removal method (Bohlin *et al.* 1989), and the mean of these three sites were used as an estimate of reach-wise annual density of Atlantic salmon. The impact of restoration on Atlantic salmon density was tested using linear mixed-effect model (LME) (Pinheiro & Bates, 2000).

4 Results and discussion

4.1 Overwintering of brown trout – emphasis on habitat structure (I,II)

The literature review indicated that there is a multitude of factors, both physical and biological, that affect the survival, behavior and habitat use of salmonids in winter. This makes interpretation of observed patterns complicated and difficult to generalize. The fact that winter seems to function as a bottleneck for the survival of young salmonids in some rivers but not in others suggests that survival may be highly context-dependent, related to the habitat characteristics and ice regimes of individual rivers. In general, overwintering salmonids are mainly nocturnal, prefer sheltered, low velocity microhabitats and interact relatively little with conspecifics or interspecifics. It is difficult to obtain a precise description of the microhabitat preferences of any given species as published results vary considerably between studies. Thus, even basic generalized winter habitat preference curves used in habitat-hydraulic modelling are almost totally lacking for young salmonids in winter (but see Mäki-Petäys *et al.* 1997, 2004; Armstrong *et al.* 2003).

The majority of research conducted on the winter ecology of salmonids has been carried out in small rivers and streams, where the temperature remains a few degrees above zero and with no ice. Very little information exists on the behavior of fish in relation to ice, and experimental research on the impact of different ice conditions on fish is almost completely lacking. Further, there is little information on overwinter survival in large rivers and in regulated rivers (Bradford 1997, Saltveit *et al.* 2001). In conclusion, this study urges research on ice dynamics and its influence on fish behavior and habitat use. There is also a shortage of knowledge about the effect of human impact on salmonid winter ecology (land-use changes, flow regulation) and continuous need to identify methods to model and assess winter habitat conditions for salmonids.

Fish in our semi-natural streams lost mass particularly during early winter. Age-0 fish in both channel treatments (channelized vs. restored) lost mass from November to January, whereas the control fish that had continuous access to food, followed a different growth trajectory, growing steadily until the end of the experiment. The channelized-stream fish lost more of their initial mass in mid winter than did the restored-stream fish (ca. 10% vs. 2.5% on average,

respectively). They then exhibited zero growth in late winter, as did also their restored-stream counterparts. By early spring (May), the channelized-stream fish had completely caught up for their greater initial mass loss compared to the restored-stream fish. At low water temperatures in early winter, Atlantic salmon tend to lose their appetite, shifting to a passive, shelter-seeking life mode (Metcalf & Thorpe 1992). However, overwintering salmonids do not completely cease feeding (Cunjak *et al.* 1987, Heggenes *et al.* 1993) and their energy acquisition and growth efficiency are considerably higher in winter at near-zero temperatures than they are for summer-acclimatized fish at 5 °C (Finstad *et al.* 2004). It therefore appears that while the early-winter mass loss in our semi-natural streams may have been partly caused by changes in photoperiod and water temperature (and consequent loss of appetite), food limitation became more important later in the winter. Because the densities of trout, as well as their invertebrate prey, in our experimental channels were closely similar to those in natural streams, our observations may translate to field conditions in boreal streams where the wintertime food supply is often inadequate to support trout growth (but see Finstad *et al.* 2004).

The relative mass loss in mid winter was greater in the channelized than in restored streams, particularly for age-0 trout. This might signal an indirect positive effect of instream restoration on the overwintering success of young salmonids, even in the absence of direct mortality costs. However, channelized-stream fish compensated rapidly for their initially greater mass loss, and by spring, there was no size difference between these two groups. It has been frequently observed that salmonids may exhibit higher than predicted growth in late winter and spring (Vøllestad *et al.* 2002, Bacon *et al.* 2005), coinciding with the mass occurrence of many invertebrates in boreal streams and rivers (e.g. Malmqvist *et al.* 2004). The greater short-term loss of body mass by age-0 trout in the channelized streams, with subsequent compensatory growth in spring, may involve costs that only appear after a time lag. Clearly, longer-term studies lasting over at least two winters are needed to better assess the potential of stream habitat restoration to improve the overwintering conditions of juvenile salmonids. In our study, the paucity of wintertime habitat caused temporary mass loss in age-0 trout, and the fast catch-up growth by the channelized-stream trout in late spring may eventually have strong negative effects on their long-term fitness (Morgan & Metcalfe 2001, Inness & Metcalfe 2008).

4.2 Evaluating the effect of in-stream restoration on salmon by habitat modeling (III)

Estimated densities of salmon parr showed no response to restoration. Salmon parr densities, derived from stocking young (age-0) hatchery-reared parr in each autumn with a constant annual stocking rate, followed the same pattern during the monitoring period in both the reference and restored reaches.

The estimated suitable habitat, measured as WUA (m^2 per 100 m river length), for young salmon peaked in all study reaches and salmon life stages at below $20 \text{ m}^3 \text{ s}^{-1}$ discharge, with restoration increasing suitable habitat more at low flows. As expected, the reference reaches showed similar WUA values between the two field measurements and modelling trials. Habitat time series over ten water years, summarized as net WUA benefit of restoration, showed significant increases in the amount of suitable habitat area under summer conditions for both age-0 and age-1 salmon parr. The reach-wise and life-stage specific increase in suitable habitat varied on average from 300 to 1000 m^2 per 100 m river length. However, restoration-induced benefits to winter habitats were marginal, with one study reach indicating even negative net WUA values. The maps visualising the spatial distribution of suitable areas for young salmon revealed that most of the areas with high WUA scores were located along river margins, both before and after the restoration, indicating that restoration measures had only limited impact on the mid-sections of the river channel.

The whole early life cycle modeling of a salmon performed in this study helps us to describe and understand the broader effects of in-stream restoration measures. According to modeled maps, the goal of restorations, i.e. increased habitat heterogeneity, was achieved. Restoration was found successful when modeled weighted usable areas are used as the 'ultimate indicator' of successful enhancement of habitats for juveniles, but only for summer conditions. The observed increase is mainly caused by the fact that restoration amplified the total wetted area for each modelled situation, a result also observed in Swedish streams after restoration (Lepori *et al.* 2005). Nonetheless, there was a dramatic shortage of wintertime WUA in River Kiiminkijoki, irrespective of in-stream restoration. This might suggest that although restoration did improve summertime rearing conditions for salmon, it was a failure in terms of improving overwintering habitat. Intuitively, increase in WUA should create potential for increased salmonid abundance but it was not observed in our pre- vs. post-restoration electrofishing surveys. The selected sites, or the selected river, had either not a

great potential for physical habitat restoration or the sites were already as good as is feasible with respect to physical heterogeneity – or the actions simply were not extensive enough.

Nevertheless, the three restored sites gained an overall theoretical 20% enhancement of the usable habitat for young salmon during the summer. This may be of crucial importance during the growing period because it may decrease intraspecific competition.

4.3 Responses of litter retention to in-stream restoration (IV)

Dredging of small streams may have altered their ecosystems because of the depletion of allochthonous organic matter (e.g. leaves) at least until mosses had re-established in the stream channels. In our experimental study, presence of mosses enhanced retentiveness of the channel considerably compared to the channelized treatment without mosses. This pattern was nevertheless not seen in the lowest flow where channels both with and without mosses were less retentive than the restored ones. Low flow is accompanied with low depth which greatly enhances the retention potential.

In the study of Muotka and Laasonen (2002), dredged channels retained leaves inefficiently at all flows whereas natural and restored channels were highly retentive in low flows and much less so at higher discharges. In this study also, the complexity of a restoration structure did not matter in low flows – all of the structures were highly retentive then. Unexpected results was seen also in the restoration study where small-wood transport distance did not decrease as an outcome of restoration (Millington & Sear 2007) hence the efficiency of the conducted restoration measures may remain low if the constructions are not extensive enough.

Gessner *et al.* (2010) identified habitat simplification as a reason for reduced litter retention that affects local invertebrate diversity with possibly large scale effects on decomposition and ecosystem functioning. Streambed structure becomes less important in high flows as retention remains low in all treatments, except in the case of high amounts of added wood. This underlines the importance of efficient retention structures in high flows.

5 Pitfalls and scenarios of habitat models

Two-dimensional habitat models are not used to estimate fish densities for specific reaches but to estimate the physical possibilities the reach has for a species. Understanding this difference is fundamental in maximizing the benefit and value of the models. Habitat hydraulic models have been used for years but development and validation of the models is still ongoing. As stated by Lahti (2009), methods for field measurements, data model creation and hydraulic modeling have neither been fully developed nor studied for the purpose of habitat modeling. The weakness of fish habitat models is the long list of assumptions that affects the validity of their predictions (Boisclair 2001). Recently, hydrodynamic habitat models have been used broadly, and they have also been evaluated with respect to simulation errors (Waddle 2010, Merckx *et al.* 2011). The models seem to be generally accurate and appropriately scaled when habitat responses over a range of flows are considered (Waddle 2010).

Scale in models and scale in combining field observations and model calculations is a constant dilemma and source of error. The more accurate three-dimensional hydraulic models should help us to understand salmonid habitat much more precisely. However, solving the physical problems associated with streambed heterogeneity sounds already complicated, and adding the problem of unqualified preferences for any species makes the task overwhelming. On the other hand, the trend in habitat modeling is towards larger scales, such as mesohabitat (MesoHABSIM, Parasiewicz 2001), or even landscapes (e.g. Meixler & Bain 2010). Changing the operative scale of models changes the nature of possible questions and answers. While larger areas can be modeled with lower costs the questions asked are different and the resolution and accuracy of the models is much reduced.

Recently, more efficient methods have been proposed for developing habitat suitability indices, such as logistic regression, discriminant analysis and artificial neural networks (see Ahmadi-Nedushan *et al.* (2006) for a review). One way is to use fuzzy logic preferences based on expert opinion rather than a massive amount of precisely measured datapoints (Jorde *et al.* 2001, Van Broekhoven *et al.* 2006, Mouton *et al.* 2007). Indeed, one of the biggest problems, and a source of uncertainty, stems from the preferences used. Most of the preferences for salmon have been collected by electrofishing and, therefore, depth preferences usually end at one meter, and velocity preferences also reflect the accessibility of different stream sections by wading. As a consequence, extreme values for depth

and velocity depend on human capabilities, possibly biasing the values for preferred and available habitats. However, Lahti (2009) validated the preference curves by Mäki-Petäys *et al.* (2002), which I also as used in my study (III). He concluded that there was a 70% higher probability to find a fish in a stream position with a high habitat value than in a low-value position. Given the high amount of assumptions at the scale of measurements, models seem to provide surprisingly good results.

A great deal of caution is needed when developing habitat hydraulic models for other, less studied species or groups, like macroinvertebrates and macrophytes. Here the scale issues become critical, as e.g. invertebrate habitat is a true microscale habitat and measuring average water column velocity is unlikely to describe successfully macroinvertebrate habitats. It has been shown, however, that even relatively coarse measurements can be used to describe invertebrate distributions (Kopecki 2008). Some large datasets about invertebrate habitat selection have been collected by using FST-hemispheres which measure near-bed hydraulic forces, showing that models based on near-bed velocities may give good results (Kopecki 2008, Sagnes *et al.* 2008). If the scale is widened to a mesohabitat scale, additional suitable studies and monitoring data can be used. As aquatic bryophytes are often key organisms of boreal stream ecosystems, modeling the moss habitat may also provide information relevant for invertebrates, possibly fish and even ecosystem function. Thus there is a need for comprehensive understanding of the stream ecosystem to direct modeling towards the most effective element.

In the future, the development and validation of habitat hydraulic models, combined with the current progress in field survey methods (laser scanning, echo sounding techniques), might lead to a wider use of models. Limited human capability to collect extensive preference data under ice, in high water velocities and deep water should encourage towards the use of modern (e.g. imaging) technologies. There will be a constant need for quantifying habitats when defining the potential for or success of stream restoration, in ecological assessment or in defining the decline of suitable habitats after human impact.

6 Restoration success: from assessment to management implications

This thesis documents both promising and relatively modest outcomes of stream restoration. Controversial findings on rehabilitation success are not exceptional, as recent meta-analyses have reported both success (Whiteway *et al.* 2010) and failure (Stewart *et al.* 2009) of fisheries enhancements. In my study, the overwintering body condition of young brown trout varied less in restored channels thus providing a possible benefit for the next growing season. However, the habitat model did not predict any significant gain in suitable habitat throughout the juvenile salmon riverine lifespan as overwintering habitat area did not increase. Neither did salmon abundance increase nor did the currently-used restoration structures enhance organic matter retention in small streams.

The key to restoration success is that the factor to be enhanced is initially limiting the population under study. After clearing the stream channels for timber transport by transferring the largest stones to the stream banks, some of the natural streambed heterogeneity was lost. Yet the decades following dredging were also characterized by extensive land use changes that modified catchment areas through forestry, ditching, peat mining and intensive farming. Clearly, all these stressors cannot be addressed only by enhancing in-stream structural complexity. However, if water quality, quantity or fish migration is not limiting, then any actions in the stream channel may produce observable benefits.

According to Stewart *et al.* (2009), in-stream devices are less effective for increasing salmonid population in large than small streams. This, however, may simply be because in small streams in-stream structures may be easily used if there is clearly a shortage of them. In larger rivers, catchment scale problems accumulate and their independent effects may be difficult to isolate. Often small-scale restorations aiming to increase structural heterogeneity should be abandoned and instead more emphasis should be placed on catchment-scale restorations (Louhi 2010). At the very least, in-stream restoration measures should be complemented by strict fisheries regulation (Syrjänen 2010). Prioritizing management actions is closely linked to the setting of restoration goals and the problems that should be solved (Wohl *et al.* 2000, Palmer *et al.* 2007).

Three studies in this thesis (I, II and III) highlight the need of knowledge on winter ecology in order to manage boreal running waters effectively. Bottleneck periods in the life cycles of many stream organisms are largely unknown, yet studies II and III indicate that life-stage specific habitat requirements might

override any effect of increased habitat heterogeneity. Overwintering habitats may limit salmonid populations in boreal streams; thus there should be a shift in restoration measures to improve habitats for all life stages of young salmonids instead of focusing on a single aspect like summer habitat. Palm *et al.* (2009) found minimum habitat suitability to explain a large portion of variation in site-specific overwintering, indicating that habitat may be the key factor for winter stationarity of individual fish. Implications of restoration for other stream biota should be taken seriously even if restoration is conducted solely for salmonid enhancement. Although possibilities to enhance benthic invertebrate communities by in-stream rehabilitation seem limited (Miller *et al.* 2010, Palmer *et al.* 2010, Louhi *et al.* 2011), a viable invertebrate community is a prerequisite for a viable salmonid population. The lack of response by macroinvertebrate communities to restoration may render them unsuitable for assessing restoration impact, thus highlighting the use of ecosystem level variables, like retention capacity, as indicators of restoration success. However, it is also possible that the lack of a positive response to restoration may be because the measures used are simply insufficient.

As shown in paper IV, the currently used restoration structures (boulders and logs) do not retain leaves effectively even at moderate flows. As a management implication, study IV suggests broader use of wood or other structures that extend beyond water surface in most flow conditions. According to study IV, stream channels should support substantially more large wood than is typically found in Finnish 'reference' streams.

It remains undefined why there is no increase in salmon juvenile densities after restoration even if the effect of spawning and migration limitations and overfishing can be excluded □ as in the case of River Kiiminkijoki where each year the same amount of juvenile salmon was stocked in each reach. It seems that suitable habitats for salmon during various life stages increased only in stream margins, as the width of the wetted area increased. And as the suitable habitats were amplified only in summer, we cannot expect an overall benefit for salmon. Moreover, the shortage of overwintering habitats may force a majority of fish to migrate and start the next growing season in a different reach (Palm *et al.* 2009). This indicates that not enough habitat enhancement effort was directed to mid-channel areas, which was most strongly affected by channelization. Also, not enough effort was directed to suitable habitats during possible bottleneck periods in the life cycle of salmon. The case study of River Kiiminkijoki presents a novel approach to in-stream restoration assessment by combining habitat modeling and

fish abundance estimation. The study points out that an apparent increase in habitat heterogeneity does not directly lead to an increase in neither suitable habitats nor salmon abundance.

The findings of this research complement an earlier review (Palmer *et al.* 2010) by emphasising that streambed complexity may not be a key factor in stream restoration projects. In the future, focus should be shifted towards larger scales, as streams face multiple stressors that need a comprehensive assessment (Ormerod *et al.* 2010). Functional connectivity to riparian habitats should be one of the priorities in stream restoration because the stream-water interface is a 'mediator' between running waters and their catchments. A large-scale positive outcome of restoration may hence be seen in the long run when banks armoured with boulders are dismantled to enable natural sediment retention and channel migration (Rosenfeld *et al.* 2011), thus restoring the riparian connectivity (as a consequence of increased wetted area). In addition to traditional active engineering, a passive restoration concept, where restoration aims to restore processes rather than habitats, has gained increasing support (Hillman and Brierly 2005, Kail *et al.* 2007). Moreover, there should be a tendency towards a comprehensive understanding of the characteristics of the river itself, because geomorphology determines largely the distribution and form of physical habitats (Brussock *et al.* 1985) and restorations should be planned in that context (Negishi & Richardson 2003).

For salmon and trout, the benefit of in-stream rehabilitation may not be detectable due to the other limiting factors or insufficient restoration measures, but the positive socio-economical outcomes of restoration (Olkio & Eloranta 2007) and the positive impact of restoration on ecosystem services (Loomis *et al.* 2000, Palmer & Filoso 2009) need also to be taken into account. It should be kept in mind that societal perceptions and expectations for ecosystem performance ultimately determine whether restoration is a viable management option (Wohl *et al.* 2005). If restoration efforts are only successful on rare occasions there is a high risk of losing societal interest towards restoration and nature conservation. This calls for a completely different approach to restoration, a fact recently stressed by Schiff *et al.* (2010).

Salmonid life cycle consists of several stages controlled by a suite of interacting variables, and a failure in any part may run a population to extinction. If the present limiting factors (e.g. overfishing; Syrjänen 2010) are removed, then in-stream habitat may become a key element for salmonids, either as suitable spawning sites, juvenile habitats or overwintering areas. Thus the actions

performed should aim at long-term benefits by using methods based on the best available knowledge rather than those traditionally used. But as long as the limiting factors are not identified and eliminated, in-stream restoration is unlikely to be a viable management action. This should encourage restoration managers to seek success through problem-oriented and catchment scale procedures.

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- I Huusko A, Greenberg L, Stickler M, Linnansaari T, Nykänen M, Vehanen T, Koljonen S, Louhi P & Alfredsen K (2007) Life in the ice lane: the winter ecology of stream salmonids. *River Research and Applications* 23: 469–491.
- II Koljonen S, Huusko A, Mäki-Petäys A, Mykrä H & Muotka T (2010) Body mass and growth of overwintering brown trout in relation to stream habitat complexity. *River Research and Applications*. In press.
- III Koljonen S, Huusko A, Mäki-Petäys A, Louhi P & Muotka T (2011) Assessing habitat suitability for juvenile Atlantic salmon in relation to in-stream restoration and discharge variability. Manuscript.
- IV Koljonen S, Louhi P, Huusko A, Mäki-Petäys A & Muotka T (2011) Quantifying the roles of in-stream habitat structure and discharge to leaf retention: implications for stream restoration. Manuscript.

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