

A close-up photograph of a brown trout swimming in a stream. The fish is positioned horizontally, facing right, with its head and eye clearly visible. It has a greenish-brown body with dark spots. The background is filled with dark, out-of-focus driftwood and rocks, creating a natural stream environment. The lighting is soft, highlighting the fish's scales and the texture of the surrounding environment.

Fine stream wood

Effects on drift and brown trout (*Salmo trutta*)
growth and behaviour

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Faculty of Health, Science and Technology

Biology

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Abstract

Stream ecosystems and their riparian zones have previously been regarded as two different ecosystems, linked through numerous reciprocal subsidies. Today, ecologists agree that the stream and the riparian zone should be regarded as one system, the stream-riparian ecosystem, which is characterised largely by the subsidies between land and water. The terrestrial subsidies to the stream affect stream-living biota in several ways, some of which are well-known while others less so. The input of wood to the stream from the riparian zone is believed to play an important role in the population dynamics of stream-living fish. In this doctoral thesis, I explore effects of fine stream wood (FW, <10 cm diameter) on wild stream-living young-of-the-year brown trout (*Salmo trutta*) by reporting and discussing results from laboratory, semi-natural and field experiments. My results show that the local density of drifting prey is higher in the presence of FW than in its absence, and also that young-of-the-year brown trout decrease their diurnal foraging time and prey capture success when FW is added to their habitat. I show that trout decrease their swimming activity in the presence of FW, aggregate in FW bundles, and have lower growth rates than trout without FW access. Also, the degree of sheltering in FW bundles was higher during day than at night in a study performed at low water temperatures; moreover, the presence of an ectothermic nocturnal predator (burbot, *Lota lota*) did not affect the degree of sheltering in FW bundles by trout. Taken together, my results indicate that young-of-the-year brown trout with access to FW bundles spend considerable amounts of time sheltering in the FW, and by doing so they miss the opportunity for higher growth and foraging rates outside of the shelter. The most probable explanation for this behaviour is that growth is traded off against survival, i.e., the predation risk is higher outside of the shelter.

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List of papers

This thesis is based on the following manuscripts and published papers, which are referred to by their Roman numerals. Paper I is reprinted with permission from Springer Verlag. Paper II, III and IV are reprinted with permission from John Wiley and Sons.

- I. Enefalk, Å. and Bergman, E. (2016). Effects of fine wood on macroinvertebrate drift in four boreal forest streams. *Hydrobiologia* **765**, 317-327.
- II. Enefalk, Å. and Bergman, E. (2015). Effect of fine wood on juvenile brown trout behaviour in experimental stream channels. *Ecology of Freshwater Fish*. doi/10.1111/eff.12244
- III. Enefalk, Å., Watz, J., Greenberg L. and Bergman, E. (2016). Winter sheltering by juvenile brown trout (*Salmo trutta*) – effects of stream wood and an instream ectothermic predator. Revised for *Freshwater Biology*.
- IV. Enefalk, Å., Huusko, A, Louhi, P. and Bergman, E. (2016). Fine stream wood decreases growth of juvenile brown trout (*Salmo trutta*). Submitted manuscript.

Contributions

Papers I and II. Åsa Enefalk had a leading role in both experiments, and Eva Bergman contributed to the planning, design, analyses and writing. Åsa Enefalk performed the field and laboratory work, collected the data, wrote the articles and performed the statistical analyses.

Paper III. Åsa Enefalk had a leading role, together with Johan Watz, in this study. All authors contributed to the development of the basic ideas and concepts and the study design. Åsa Enefalk and Johan Watz performed the fieldwork, collected approx. 90% of the laboratory data used, and ran the statistical tests. Johan Watz took the largest part in the statistical analysis, and Åsa Enefalk wrote the manuscript. Eva Bergman, Johan Watz and Larry Greenberg made valuable comments for improving the article.

Paper IV. Åsa Enefalk had a leading role in this study. Åsa Enefalk, Ari Huusko and Eva Bergman contributed to the development of the basic ideas and concepts and the study design. Åsa Enefalk and Ari Huusko performed the fieldwork together with the staff at Paltamo research station. Pauliina Louhi selected the statistical method and ran most of the statistical tests. Åsa Enefalk performed most of the laboratory work and wrote the manuscript, and all co-authors made valuable comments for improving the article.

Introduction

Stream ecosystems and their riparian zones have previously been regarded as two different ecosystems, linked through numerous reciprocal subsidies. During the last decades, ecologists have concluded that the stream and the riparian zone should be studied as one system, the stream-riparian ecosystem, which is characterised largely by the subsidies between land and water (Gregory *et al.*, 1991; Wallace *et al.*, 1997; Nakano & Murakami, 2001; Baxter, Fausch & Carl Sanders, 2005). Management of riparian zones in forested watersheds will affect a wide range of environmental variables in streams, such as water discharge, light inflow, thermal regime, nutrient flux and terrestrial subsidies of energy and resources (Schlosser, 1991; Goodwin, Hawkins & Kershner, 1997; Richardson, Zhang & Marczak, 2010; Broadmeadow *et al.*, 2011). Changes in these environmental variables can have pervasive effects on stream biota. In small forest streams, for example, relatively moderate changes in the riparian zone can affect prey availability, and thereby also distribution and production of stream fish (Kawaguchi, Taniguchi & Nakano, 2003; Ward, Nislow & Folt, 2009; Urabe *et al.*, 2010). The mitigation of anthropogenic and climate-change impacts on stream-riparian ecosystems relies on optimal and adaptive management, highlighting the need for identifying the ecological functioning of inputs from the riparian zone to the stream.

Stream fish often depend on overhead cover and instream sheltering structures which originate from the riparian zone, i.e. stream wood and riparian vegetation (Whiteway *et al.*, 2010; Jonsson & Jonsson, 2011). The availability of fine stream wood (FW; <10 cm diameter) is considered to be important for small-sized stream-living fish (Culp, Scrimgeour & Townsend, 1996) and for invertebrates (Spänhoff & Cleven, 2010), but little is known about the ecological role of FW in small streams in northern Europe. The input of FW to streams, and the functionality of FW in streams, will likely change in the future due to changed forestry practices and disturbance patterns (Hansson 2010 *and references therein*; Vaz *et al.*, 2013). Therefore, an understanding of the role of FW in stream ecosystems is needed to predict how salmonid populations will respond to these changes. This understanding is important as an efficient management of salmonid populations will be crucial to preserve the dynamics of entire stream

ecosystems, which are deeply influenced by the presence of salmonids and other top predators. In this doctoral thesis, I report results from experimental and field studies in which I have examined the role of FW in the first year of life of resident brown trout (*Salmo trutta*), focusing on effects on behaviour, growth and prey availability.

Stream wood and stream invertebrates

Stream wood is a key component of forest streams, influencing a range of ecosystem properties, such as retention of energy and material (Bilby & Ward, 1989; Muotka & Laasonen, 2002), water depth and flow patterns (Riley & Fausch, 1995; Keim, Skaugset & Bateman, 2002), as well as the amount of cover and habitat complexity available to stream-living biota (Lester, Wright & Jones-Lennon, 2007; White *et al.*, 2011). Most research on stream wood concerns large wood (LW; >10 cm in diameter) in western North America (e.g., Robison & Beschta, 1990; Riley & Fausch, 1995). Effects of fine stream wood (FW) are less well known.

In the 1950s, large-scale forestry was introduced, which was a shift from the felling of selected trees to clear-cut felling of large areas. Furthermore, since the 1990s, biofuel has been an increasingly important forestry product (Heinimö *et al.*, 2011). These two changes in forestry practices have resulted in an extensive removal of wood from forest ecosystems (Crisp, Eriksson & Peter in Northcote & Hartman, 2008). Thus, the outtake of FW from Swedish forests has increased three-fold during the last two decades (Hansson 2010 *and references therein*), and one pathway of energy and material between riparian zones and streams has been weakened. Wood that earlier would have fallen into the stream is instead used for human purposes.

Stream-living salmonids are believed to benefit from the presence of instream structures, and should thus be negatively affected by removal of stream wood. Investigations have, however, indicated positive, equivocal or negative responses of stream salmonid abundance and biomass to streamside logging and removal of large stream wood (Mellina & Hinch, 2009; Stewart *et al.*, 2009; Whiteway *et al.*, 2010). The effect of changes in LW input seems to be dependent on time since logging, ontogenetic stage of the fish, and stream characteristics (Mellina & Hinch, 2009; Whiteway *et al.*, 2010). Concerning removal of FW, effects on stream salmonids are not well-

known, but studies have revealed negative effects on density and diversity of stream invertebrates (Siler, Wallace & Eggert, 2001; Spänhoff & Cleven, 2010).

Fine stream wood and other in-stream structures are colonised by stream invertebrates, as they can serve as sites for oviposition and attachment (Peckarsky, Taylor & Caudill, 2000), increase the availability of resources, and provide shelter from predators (Crowder & Cooper, 1982; Schneider & Winemiller, 2008). Filtering invertebrates colonise the wood surface soon after the wood enters the water; thereafter, the wood is colonised by biofilm consisting of bacteria, algae and fungi (Golladay & Sinsabaugh, 1991; Couch & Meyer, 1992) and finally by invertebrates from other functional groups than filterers. Invertebrates colonise the wood surface during a period of 3 weeks – 3 months, whereafter their density levels off or decreases (Nilsen & Larrimore, 1973; Drury & Kelso, 2000; Bond *et al.*, 2006; Spänhoff & Cleven, 2010). Fine wood removal can reduce both benthic and drift abundance of stream-living invertebrates (Wallace *et al.*, 1999; Siler *et al.*, 2001). Different invertebrate functional groups seem to respond differently to FW removal, with negative effects mainly on filterers and gatherers, while the effects on scrapers vary, probably due to varying effects of FW on light input to the benthos (Behmer & Hawkins, 1986; Wallace *et al.*, 1999; Siler *et al.*, 2001).

Young-of-the-year brown trout

Shelters and sheltering

Sheltering structures have a pervasive effect on stream-living animals, as they affect distribution as well as growth rates, stress level, prey abundance, survival and behaviour (Sundbaum & Näslund, 1998; Armstrong & Griffiths, 2001; Siler *et al.*, 2001; Näslund *et al.*, 2013). Sheltering behaviour in salmonids has several causes, e.g., avoidance of adverse environmental conditions such as strong currents, or avoidance of aggressive conspecifics or predators (Imre, Grant & Keeley, 2002). The degree of sheltering is often related to light conditions and water temperature (Cunjak, 1988; Metcalfe & Steele, 2001), but also to the type of available shelters (Jonsson & Jonsson, 2011). The type of sheltering structures affects the degree of sheltering

in several ways, including the preference of small-sized fish to use small-sized shelters (Culp *et al.*, 1996; Howson *et al.*, 2012).

In salmonids, juveniles prefer to shelter in small structures such as FW or river mosses, but tend to avoid LW and boulders which are instead used by older, larger salmonids (Culp *et al.*, 1996; Whiteway *et al.*, 2010; Langford, Langford & Hawkins, 2012). Juvenile salmonids may also shelter close to cobbles (Jonsson & Jonsson, 2011), and in microhabitats with low light levels, such as streambed interstices (Griffith & Smith, 1993; Heggenes *et al.*, 1993; Valdimarsson & Metcalfe, 1998). River mosses and other aquatic macrophytes are often lacking in shaded nutrient-poor streams (Riley *et al.*, 2009). In their absence, FW may play an important role as shelter for small trout.

Sheltering structures have been proposed to increase salmonid survival both directly, by decreasing predation rates, and indirectly, by increasing individual energetic performance (Finstad *et al.*, 2007), partly because of reduced standard metabolism and stress levels (Millidine, Armstrong & Metcalfe, 2006; Näslund *et al.*, 2013). Reduced standard metabolism can, however, affect survival and energetic performance both positively, negatively or not at all; also, the effect differs among environments (Harwood *et al.*, 2003; Burton *et al.*, 2011; Reid, Armstrong & Metcalfe, 2012). The effect of sheltering structures on growth and survival may also be mediated by other mechanisms than reduced metabolic rates and predation risk, such as increased prey abundance.

Predation

Predation risk is generally affected by availability of habitat structures (Lima, 1998). Use of shelter reduces the rate of mortality by predation (Godin, 1997), but simultaneously reduces foraging and growth, which can have long-term negative effects on survival (Sih, 1980 and 1997; Sih, Petranka & Kats, 1988; Lima & Dill, 1990). In salmonids, lower growth rates have been recorded when piscivorous predators are present (Reinhardt, Yamamoto & Nakano, 2001; Álvarez & Nicieza, 2003), and reduced growth rates in sheltering animals may be the result of a trade-off between foraging and survival (Lima & Dill, 1990; Werner & Anholt, 1993; Dmitriew, 2011).

Juvenile salmonids experience predation from a range of animals differing in foraging behaviour and physiology (Harvey & Nakamoto, 2013), i.e. endothermic terrestrial predators attacking from the air (e.g. brown bear, *Ursus arctos*, and grey heron, *Ardea cinerea*; Gard, 1971; Carss, 1993), ectothermic aquatic predators (pike, *Esox lucius*, and burbot, *Lota lota*; Kahilainen & Lehtonen 2003; Hyvärinen & Vehanen, 2004) and land-living predators that are able to forage under water, and are either endothermic (e.g. American mink, *Neovison vison*, Heggenes & Borgström, 1988) or ectothermic (e.g. European ringed snake, *Natrix natrix*; Gregory & Isaac, 2004). Different predators are supposed to influence the activity patterns of their prey in different ways. Predators foraging by vision represent a greater threat in daylight than in darkness, and this has often been suggested to explain night-time foraging and day-time sheltering in salmonids (Cunjak, 1988; Metcalfe & Steele, 2001). However, the behavioural response to visual predators may vary widely, e.g. presence of pike caused brown trout to become less nocturnal (Vehanen & Hamari, 2004), while presence of piscivorous brown trout instead caused juvenile trout to become more nocturnal (Álvarez & Nicieza, 2003).

Water temperature affects the level of predation risk and the effect of predation risk on habitat use. During winter, juvenile salmonids experience a more serious threat from endothermic predators than during summer (Heggenes & Borgström, 1988; Harvey & Nakamoto, 2013). Ectothermic predators are less active during winter than endothermic ones, but this difference between ectothermic and endothermic predators is reduced during warm winters when water temperatures are higher (Huusko *et al.*, 2007), as ectothermic predators then need more energy and are able to increase their activity level.

Growth

The growth rates of brown trout influence fitness by affecting reproductive success and survival rate. The most important factors determining growth rates in juvenile stream-living salmonids are temperature (Connor *et al.*, 2002), prey availability (Ward *et al.*, 2009) and fish density (Jenkins *et al.*, 1999; Grant & Imre, 2005; Vøllestad & Moland Olsen, 2008). In addition, individual foraging behaviour and metabolic rate interact with prey availability in

influencing growth rates (Burton *et al.*, 2011; Hoogenboom *et al.*, 2013). Temperatures for optimal growth are generally low for salmonid fish; growth rates for stream-living brown trout increase with temperature from 5 to approx. 13°C, which is lower than the optimal temperature for growth of trout in lakes and seas (Elliott, Hurley & Fryer, 1995; Forseth *et al.*, 2009). At low temperatures during winter, growth ceases and variation in energetic performance is instead manifested in varying mass loss rates (Finstad *et al.*, 2007). Access to instream shelters, e.g. FW, may affect growth and activity patterns in stream-living salmonids by affecting the trade-off between foraging and sheltering, resulting in an increased degree of sheltering and therefore reduced foraging. Shelter availability can also reduce growth by density-dependent effects inside the shelters (Teichert *et al.*, 2010). Effects of fish density on growth are easier to detect at relatively low fish densities (<1 fish·m⁻²; Grant & Imre, 2005; Lobón-Cerviá, 2005), but are supposed to also exist at higher fish densities (Jonsson & Jonsson, 2011). However, results from studies performed at low water temperatures have indicated stronger density dependence – higher mass loss rates – in Atlantic salmon (*Salmo salar*) in shelter-poor than in shelter-rich environments (Finstad *et al.*, 2007 and 2009). Furthermore, density dependent effects on growth are related to the ontogenetic state of the fish. In Atlantic salmon, density dependent effects on growth rates increase 2 – 3 months after the initiation of external feeding (Einum, Sundt-Hansen & Nislow, 2006).

Foraging and diet

Brown trout most often forage by holding a position in the stream, from which they catch both drifting and epibenthic prey (Elliott, 1994). Their growth and the composition of their diet are strongly affected by prey availability (Sagar & Glova, 1992; Ward *et al.*, 2009; Syrjänen *et al.*, 2011). When trout start exogenic feeding in early summer, they feed almost exclusively on stream invertebrates, e.g. chironomid larvae and pupae (Jonsson & Gravem, 1985) or *Ephemerella* larvae (Kreivi *et al.*, 1999), depending on prey availability in the stream. During their first autumn, Trichoptera larvae become common in their diet (Jonsson & Gravem, 1985; Kreivi *et al.*, 1999). In winter, appetite is lower (Metcalf & Thorpe, 1992), and salmonids are less dependent on drifting prey and more often

feed on epibenthos (Kreivi *et al.*, 1999). Also, salmonids increase their nocturnal activity at low water temperatures (Cunjak, 1988; Heggenes *et al.*, 1993; Fraser, Metcalfe & Thorpe, 1993; but see Larranaga & Steingrímson, 2015), and the preference for foraging at low light levels decreases the efficiency of drift feeding (Watz & Piccolo, 2011). In brown trout, drift feeding may also be impeded when the trout shelter in a highly structured habitat, as has been shown for foraging of other visual predators such as the largemouth bass (Gotceitas & Colgan, 1989). Also, sheltering structures may decrease water velocity and thereby the flux of drifting prey, and a high level of structure may physically impede drift foraging (O'Brien & Showalter, 1993; Gustafsson, Greenberg & Bergman, 2012).

Objective

The objective of this doctoral thesis was to evaluate different effects of FW availability on resident young-of-the-year brown trout, *Salmo trutta*, in small boreal forest streams (Fig. 1). More specifically, I aimed to answer the following research questions: Does FW affect juvenile brown trout by effects on 1) the density or biomass of drifting invertebrate prey? 2) trout diet and foraging behaviour? 3) anti-predator response of trout? and 4) trout growth rates? I performed experiments in the laboratory, field and under semi-natural conditions to address these questions, and the results are reported in four papers: Paper I reports the results from a field experiment where FW density was manipulated at seven sites in four boreal forest streams. In that paper, I evaluated the effects of FW presence on prey availability of young trout, i.e. on the density, diversity and biomass of drifting invertebrates. The laboratory study reported in Paper II tested the behavioural response of foraging young-of-the-year trout to three FW densities and two fish densities, while the laboratory study in Paper III tested the sheltering behaviour of young-of-the-year trout at low water temperatures, during day and night, in the absence and presence of an instream ectothermic predator, and in the absence and presence of FW bundles. Paper IV is based on a joint project by Karlstad University and the Natural Resources Institute Finland (Luke) in Paltamo, and reports effects of FW availability on young-of-the-year brown trout growth, prey availability, position choice and diet.



Fig. 1. Brown trout was chosen as study species. The photograph shows a ten-month-old trout from the resident population in River Barlingshultsälven, Värmland, Sweden (Photo A. Tedeholm).

Methods

The studies in this thesis were conducted in the field and in artificial indoor and outdoor streams from June 2011 to March 2015. All studies used wild or semi-wild young-of-the-year brown trout as study fish (Fig. 1, Table 1).

Study sites

The field study on drifting invertebrates (Paper I) was conducted in Värmland county, Sweden, from June to August 2011 in four small streams (catchment area 9 – 16 km², mean water velocity 0.2 – 0.5 m·s⁻¹). The laboratory experiments relating to FW effects on trout behaviour were carried out in the aquarium facility at Karlstad University during November – December 2012 (Paper II) and January – March 2015 (Paper III). The study of trout growth and diet (Paper IV) was performed during August – December 2013 in semi-natural stream channels located at the National Resources Institute Finland, Paltamo, Finland (64°24'N, 27°31'E; Table 1).

Stream invertebrate drift

I used drift nets to study effects of FW on stream invertebrate drift in the field (Paper I). One drift net was set upstream of a tethered birch branch bundle (*Betula pubescens*) and another downstream of the same bundle. This was done at seven sites in four small forest streams. Drift was sampled on five dates during the summer of 2011 from mid-June, two weeks after FW addition, to mid-August, ten weeks after FW addition (water temperatures 15 – 18°C). FW volume per bundle was approx. 8 dm³. Invertebrates were sorted and weighed ≤24 hours after they were collected. Thereafter, they were preserved in 70% ethanol. In the laboratory, I counted the individuals of each sample and identified their taxa. To compare upstream and downstream samples, I calculated drift density (individuals·100 m⁻³ of water), drift wet mass (mg·100 m⁻³ of water) and Shannon-Wiener indices.

Behaviour

Effects of FW on the behaviour of young-of-the-year brown trout were studied in four 7 m long indoor experimental streams at Karlstad University (Papers II and III; Table 1). For both experiments, I used the run compartments of the streams, measuring 1.85×0.95 m, and FW from bundles previously used in the drift study (Paper I). I studied foraging and sheltering behaviour of 36 trout, electro-fished from River Tvärån, by tagging them with visible implanted elastomers and thereafter video-recording them during drift feeding on thawed bloodworms (Chironomidae). The trout were observed alone and in groups of four individuals (Paper II). Three FW densities were used in this study (0, 1.2 and $9 \text{ dm}^3 \cdot \text{m}^{-2}$ of stream bottom area) and water temperature was 13°C . To examine anti-predatory behaviour, I performed a laboratory study at low water temperatures (5.5°C) by PIT-tagging 46 trout electro-fished from River Barlingshultsälven, and tracking them with a PIT-antenna in daylight and darkness, and in the presence or absence of an instream ectothermic predator (burbot; Paper III). In this study, all treatments contained shelters in streambed interstices, and all trout were tested at two FW densities (0 and $5 \text{ dm}^3 \cdot \text{m}^{-2}$ of stream bottom area). Trout were tested in groups of three individuals.

Growth, diet and distribution

Brown trout growth rates, diet and distribution were studied by monitoring 360 PIT-tagged trout in six outdoor semi-natural stream channels. The trout were kept in tanks from hatching to the late yolk-sac phase, and thereafter in the channels used in the experiment. Each channel was divided into 3 sections (8.5×1.5 m), where each section received 20 trout, and half of the sections received FW bundles (*Salix* sp., $5 \text{ dm}^3 \cdot \text{m}^{-2}$ of stream bottom area; Paper IV, Table 1, Fig. 2). Trout growth was measured for the periods late summer – early autumn, early autumn – late autumn and late autumn – early winter, as well as for the entire study period late summer – early winter (water temperature decreasing from 17 to 1°C). Trout were stomach-flushed in early autumn, late autumn and early winter. Their gut contents were analysed for proportion of occurrence of the most common taxa, and also for ethanol-preserved wet mass. Furthermore, invertebrates were sampled, and the position of trout was determined on two occasions in autumn and one in early winter.



Fig. 2. One of the six channels in the outdoor stream channel facility used in the study described in Paper IV. White arrows point to the construction where the two fences between the sections were to be fixed. In this channel, the most upstream section had received a load of FW, weighed down by stones for the first couple of weeks until the wood remained submerged by itself.

Table 1. Summary of the experimental design and fish used in the studies described in papers II, III and IV.

Paper	Treatments	Response variables	FW density (dm ³ ·m ⁻²)	FW species	Brown trout	Fish density (ind·m ⁻²)	n	Length (mm; mean±SD)	Mass (g; mean±SD)
II	Fine wood (3 levels; no, intermediate and high FW density) No. of fish (2 levels; 1 and 4 fish)	Sheltering	1.2	<i>Betula</i>	0+	0.6	36	61 ± 7.2	2.5 ± 0.96
		Aggression	and	<i>pubescens</i>	wild	&		(fork length)	
		Feeding success	9			2.3			
		Time spent foraging			origin River Tvärån				
III	Fine wood (2 levels; present or absent) Predator (<i>burbot</i> , 2 levels; present or absent) Light (2 levels; daylight or darkness)	Swimming activity							
		Sheltering in streambed and fine wood	5	<i>Betula pubescens</i>	0+ wild	1.7	46	73 ± 5.9 (total length)	3.4 ± 0.9
					origin River				
					Barlingshults älven				
IV	Fine wood (2 levels; present or absent)	Growth	5	<i>Salix</i> sp.	0+	1.7	360	78 ± 5.0 (fork length)	5.0 ± 1.1
		Distribution			semi-wild				
		Diet							
		Prey availability							

Summary of results

The presence of submerged FW bundles in the streams resulted in increased density of drifting invertebrates. Young-of-the-year brown trout sheltered extensively in FW, and reduced their foraging success, activity level, growth rates and the time spent sheltering in the streambed (Table 2).

Paper I

Drift density of aquatic invertebrates in this field study was generally low, with median values over the sampling season of 0.9 – 1.9 individuals $\cdot 100\text{m}^{-3}$ of water. Drift density was significantly higher downstream than upstream of the FW bundles on the last sampling date, ten weeks after FW addition (median: 5.5 times higher; Fig. 3). Six out of seven sites also had higher aquatic drift biomass downstream of the FW ten weeks after FW addition (median: 8.2 times higher; Fig. 3). Biodiversity of aquatic taxa, calculated as Shannon Wiener indices, did not differ upstream and downstream of the FW bundles ten weeks after FW addition. Aquatic larvae of Diptera and Plecoptera were more frequent downstream than upstream of the FW bundles, when including the entire sampling period in the analysis.

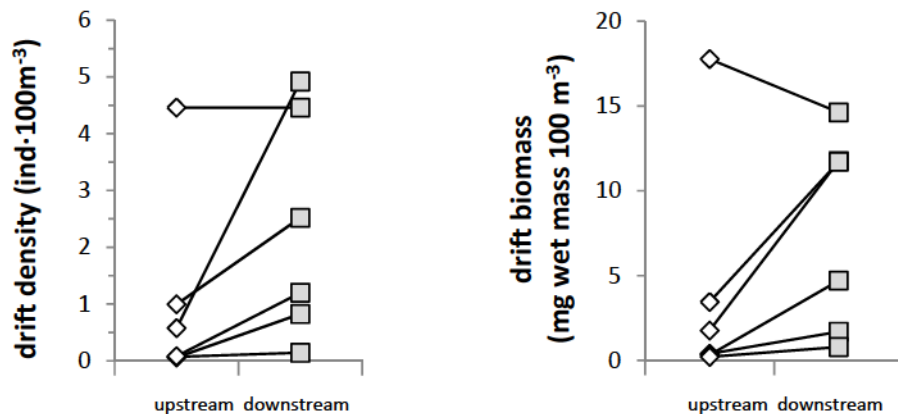


Fig. 3. Data of drift density (number of individuals belonging to aquatic taxa $\cdot 100\text{ m}^{-3}$) and biomass (mg wet mass belonging to aquatic taxa $\cdot 100\text{ m}^{-3}$) upstream and downstream of FW bundles ten weeks after FW addition. Lines connect the upstream and downstream data point of each sample site. Figure modified from Paper I.

Table 2. Summary of results from the studies described in Papers I-IV, detailing dependent and significant explanatory variables ($\alpha=0.05$).

Study	Treatments	Dependent (significant explanatory variables)	Comment
I	Fine wood	Drift of aquatic macro-invertebrates	Increased drift density (individuals/volume) downstream of fine wood More Diptera and Plecoptera larvae downstream of fine wood
II	Fine wood Presence/absence of conspecifics	Sheltering Feeding success Time spent feeding Swimming activity	Higher degree of sheltering at high FW densities Lower feeding success and rate at intermediate than no FW density Lower activity in FW treatments than at no FW density Lower activity when trout were alone
III	Fine wood Light Predator presence Fine wood \times light	Sheltering in streambed and fine wood	Decreased sheltering in streambed in FW presence, and more so in daylight Decreased sheltering in streambed in predator presence Increased sheltering in streambed and FW in daylight
IV	Fine wood	Growth Distribution Diet	Slower growth in FW treatments Aggregation of trout in FW bundles Lower consumption of chironomid larvae in FW treatments in winter

Paper II

In this laboratory study, the mean percentage of time spent **sheltering** by brown trout was higher at a high FW density than at an intermediate FW density (83% vs. 59%). **Foraging success** (prey capture success and time spent for successful attacks on prey) was lower at an intermediate FW density than in a microhabitat without FW (mean values 2.5% and 0.7% of the trial time spent catching prey at no and intermediate FW density, respectively; 90% and 50-67% of attacked prey caught). Presence of FW and absence of conspecifics both reduced the proportion of time the fish spent **cruising** (swimming at the speed $0.5 - 2$ fish body-lengths·s⁻¹; mean values 2.4% at the no FW density, 0.8% and 0.5% at the intermediate and high FW density; 0.9% when trout were alone, 1.5% in groups of four). Thus, the laboratory tests revealed that access to FW influenced the behaviour of young-of-the-year brown trout.

Paper III

Presence of FW decreased the degree of sheltering in the streambed at low water temperatures by a factor of 2.2 in daylight and a factor of 1.5 in darkness (Fig. 4). Presence of an instream ectothermic predator (burbot) did not affect sheltering in FW but reduced sheltering in the streambed by a factor of 2.4 in darkness and 1.6 in daylight (Fig. 4).

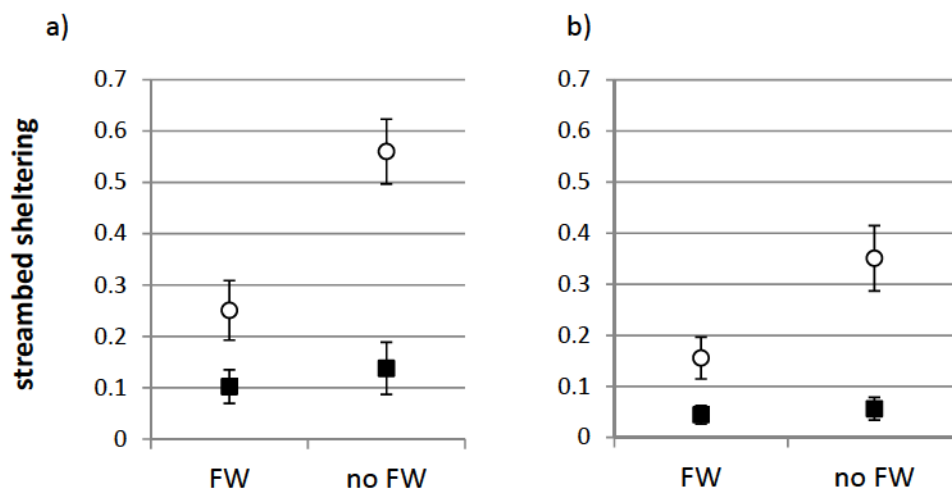


Fig. 4. Streambed sheltering, a) no predator present and b) a burbot present. Mean ± 1 SE of the proportion of observations. Open circles for daylight, filled squares for darkness. $n=22$ for the treatments without burbot, $n=21$ for burbot+FW, $n=24$ for burbot with no FW.

Sheltering in FW was 1.3 times more common in daylight than in darkness. Thus, presence of FW and a fish predator influenced when and where young-of-the-year brown trout were seeking shelter.

Paper IV

Trout in semi-natural outdoor streams grew approx. 1.2 times faster in the absence of FW than in its presence during the period late summer – early winter (Fig. 5). The most commonly occurring prey items in the trout diet were case-bearing and free-living Trichoptera larvae in autumn (found in 50-80% of the trout guts), and Ephemeroptera and chironomid larvae in early winter (in 30-60% of the guts). In early winter, twice as many trout in control treatments consumed chironomid larvae, and in late autumn, 1.5 times more trout in FW treatments consumed Ephemeroptera larvae. FW availability did not affect gut fullness. The daylight distribution of trout with access to FW differed from the distribution of trout without FW access, as on average 66% of the trout individuals in sections with FW were located underneath the FW bundles, while individuals in control sections were distributed relatively evenly over the entire channel section. Thus, presence of FW influenced the diet and spatial distribution of young-of-the-year brown trout during the day, and also reduced growth of young-of-the-year brown trout.

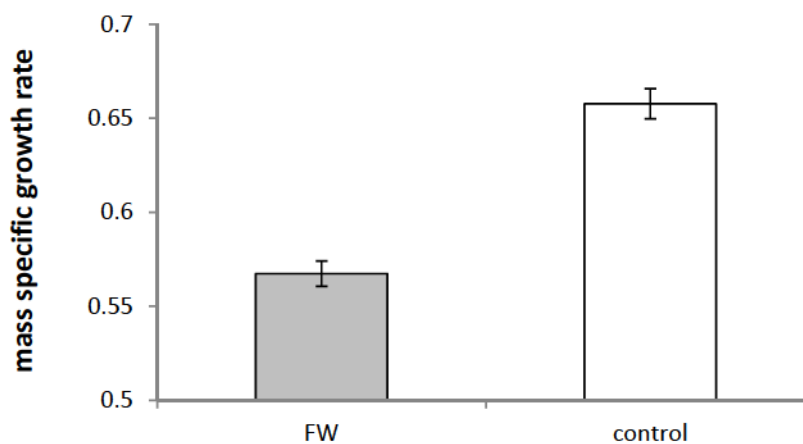


Fig. 5. Mass-specific growth rates ($\Omega\%$) of trout (mean \pm 1SE) during late summer – early winter in FW (grey) and control (white) sections. $n=9$ for FW, $n=9$ for control.

Discussion

Stream fish are highly affected by the presence of sheltering structures, as shelters potentially influence fish growth, prey availability, foraging success and predation risk (O'Brien & Showalter, 1993; Siler *et al.*, 2001; Teichert *et al.*, 2010). Earlier studies on effects of stream wood on salmonids have focused mainly on wood ≥ 10 cm in diameter and fish ≥ 10 cm. This thesis examines the effects of FW ≤ 2 cm in diameter on young-of-the-year brown trout 4 – 9 cm long. Thereby, I extend previous work on the response of stream-living salmonids to instream structure (Imre *et al.*, 2002; Whiteway *et al.*, 2010; Langford *et al.*, 2012) and on the ecological role of FW in streams (Drury & Kelso, 2000; Spänhoff & Cleven, 2010; Vaz *et al.*, 2014). Moreover, the thesis contributes to our understanding of FW as a shelter affecting behaviour and growth of juvenile stream salmonids (Papers II, III and IV) as well as describes the role of FW as a source of drifting invertebrate prey (Paper I).

From the combined results of the studies included in this thesis, the following conclusions can be made:

- 1) Prey availability for young-of-the-year brown trout can be enhanced by the presence of FW, at least locally and approx. 2 months after FW enters a boreal stream.
- 2) In the presence of FW, young-of-the-year brown trout reduce their swimming activity and aggregate in FW bundles. In addition to reduced activity levels, FW decreases foraging by reducing capture success and the time spent foraging.
- 3) The degree of sheltering in FW bundles at low water temperatures is unaltered by the presence of a night-active instream ectothermic predator, and is higher in daylight than in darkness, maybe because sheltering in FW primarily offers protection from day-active terrestrial endothermic predators. In contrast, the degree of sheltering in the streambed is reduced by the presence of FW and also by the presence of an instream ectothermic predator.
- 4) Access to FW decreases growth rates in juvenile stream-living brown trout during their first autumn and the onset of their first winter, probably as a result of density dependence inside the FW shelters when the survival benefits of sheltering are traded off against foraging and growth.

In the four boreal forest streams (Paper I), stream invertebrate drift density was higher downstream than upstream of FW bundles 8 – 10 weeks after FW addition, and drift biomass tended to be higher downstream of FW bundles. The increased drift indicates that addition of FW can locally enhance prey availability of brown trout, but the response of drifting invertebrates to the presence of FW bundles is likely related to the time elapsed since FW addition. My results agree with reported peaks in benthic invertebrate density 3 weeks – 3 months after addition of instream structure (Drury & Kelso, 2000; Bond *et al.*, 2006; Spänhoff & Cleven, 2010). Earlier studies also report higher benthic and drift densities of shredders, gatherers and filterers when FW is present (Behmer & Hawkins, 1986; Wallace *et al.*, 1999; Siler *et al.*, 2001), which is corroborated by unpublished data from my field study. However, my study focused on short-term local effects of FW presence. Short-term increases in drift density close to FW bundles are probably caused by re-distribution and aggregation of invertebrates, which in turn may cause an aggregation of juvenile trout, and thereby possibly an increased intra-specific competition for invertebrate prey. Potential long-term effects of FW addition on the invertebrate drift of entire stream reaches may eventually result in increased population sizes of brown trout, but are beyond the scope of this thesis.

Juvenile trout used FW extensively as a shelter at a wide range of temperatures, both in laboratory streams and in outdoor stream channels (Papers II, III and IV). At low water temperatures, however, the degree of sheltering in FW was lower in darkness than in daylight, indicating an effect of light levels on FW use (Paper III). The great proportion of time spent sheltering in FW resulted in lower swimming activity than in microhabitats lacking FW (Paper II). These results are consistent with results from earlier studies detecting aggregation of juvenile rainbow trout (*Oncorhynchus mykiss*) in FW (Culp *et al.*, 1996), generally high densities of small-sized fish individuals in FW microhabitats (5 – 12 cm long fish; Howson *et al.*, 2012), and decreased activity levels in brown trout when large stream wood is present (Gustafsson, Greenberg & Bergman, 2012). I also found that trout with access to FW spent less time foraging and were less successful in catching drifting food items than in microhabitats without FW (Paper II), which corroborates earlier research reporting reduced reaction distances and foraging rates in highly structured

habitats (Savino & Stein, 1982; Wilzbach, Cummins & Hall, 1986; O'Brien & Showalter, 1993; Sundbaum & Näslund, 1998; Venter *et al.*, 2008). These consistencies suggest that the presence of habitat structure can have important effects on fish distribution and foraging, not only in brown trout but also in several other fish species.

In Paper IV, I found changes in the daytime distribution of juvenile brown trout when FW was added, as the trout aggregated in the FW bundles. This effect is probably caused by several mechanisms, which include the possibility to reduce encounter rates with predators by sheltering (Boström & Mattila, 1999; Templeton & Shriner, 2004). Surprisingly, when I tested the behavioural response of trout to an instream, nocturnal, ectothermic predator at low water temperatures (Paper III), predator presence did not increase the degree of sheltering. Instead, the presence of this type of predator reduced the degree of sheltering in the streambed and did not affect sheltering in FW bundles. A possible explanation for this is that the use of FW and streambed shelters mainly provides protection from day-active endothermic predators (Heggenes & Borgström, 1988; Cunjak, 1988; Metcalfe & Steele, 2001). Another mechanism causing aggregation of trout in FW bundles could be the possibility to benefit from a higher local prey abundance, paralleling the higher drift density found in Paper I. FW added more surface area to the microhabitat, resulting in more substrate available for invertebrates and potentially higher numbers of invertebrate individuals in FW microhabitats. However, this did not result in higher growth rates of brown trout in FW microhabitats. Instead, brown trout in FW sections grew slower than those in control sections. Also, samples of the invertebrate fauna on FW surfaces and bottom gravel indicate that the density of invertebrates was lower on FW than on gravel in autumn (Paper IV). Thus, my results suggest that trout most probably do not benefit from a higher prey density in FW microhabitats, at least not when 1) the FW was added to the habitat ≤ 4 months ago, and 2) during the first autumn of the trout.

I have no clear answer as to why trout growth in the FW microhabitats was slower than in open habitats (Paper IV). One possibility is that the prey encounter rate decreased because the movements of the trout were so low while sheltering in FW (cf. Mittelbach 1981). If the encounter rate is low enough, energy

consumption may be reduced to an extent that exceeds the energy gained by less swimming. Alternatively, growth may be restricted by a high local fish density (Teichert *et al.*, 2010; Orrock *et al.*, 2013; Kiffney *et al.*, 2014). The decrease in growth was significant only when the entire period from late summer to early winter was analysed, and this effect was not evident within sub-periods. The reduction of growth rates during late summer to early winter is in agreement with studies reporting that density dependent effects in salmonids may generally be weak during the first months after emergence, and increase after the first summer (Einum *et al.*, 2006; Hoogenboom *et al.*, 2013). However, other studies have found no reduced growth in complex habitats, but instead positive effects of shelter access on energy budgets of juvenile salmonids, i.e., faster growth, lower mass loss rates and reduced resting metabolism (Millidine *et al.*, 2006; Finstad *et al.*, 2007; Hoogenboom *et al.*, 2013). These positive effects of shelter access contradict the slower growth found by me and others (Teichert *et al.*, 2010; Orrock *et al.*, 2013; Kiffney *et al.*, 2014), but the varying results are most probably caused by differences in fish studied, response variables chosen, and experimental designs. The use of small fry (Hoogenboom *et al.*, 2013) may mean that the fish have not reached the ontogenetic state when density dependent effects on growth increase (Einum *et al.*, 2006), and single fish (Millidine *et al.*, 2006) will probably respond differently to shelter access than fish in groups of conspecifics (Paper IV). Also, the sheltering fish in my studies may have benefitted from reduced standard metabolism, as found by Millidine *et al.* (2006) for juvenile Atlantic salmon with shelter access, but the positive effects on energy budgets may have been overruled by the increase in local density of trout (Paper IV). Interestingly, Finstad *et al.* (2007) found effects of shelter access on mass loss rates only when shelters of a certain size were used. Taken together, there is much variation in the results reported in the literature considering effects of instream structure on energy budgets and growth of juvenile salmonids. This variation highlights the need for systematic studies on the effects of environmental heterogeneity on growth and performance of different life stages of salmonids.

Under semi-natural conditions (Paper IV), the trout spent four months together in groups of twenty fish, each group residing in one 8.5 m long enclosed stream section. The trout should thus have been

familiar with each other. Familiar salmonid individuals are not expected to use much energy on competition, territoriality or aggression (Griffiths *et al.*, 2004), and familiarity has even been suggested to explain why resident brown trout exhibit higher growth rates than migratory trout (Závorka *et al.*, 2015). This indicates that the slower growth of trout in FW microhabitats (Paper IV) was probably not caused by competition for space among sheltering fish inside the FW bundle. The slower growth may instead have been caused by competition for food, or by decreased foraging in FW microhabitats for some other reason (Paper II). However, competition for food and decreased foraging should have resulted in lower gut fullness of trout with access to FW, but in the three diet samplings used in the study reported in Paper IV, I found no such effects. Maybe there were some differences in the amount of food consumed between the trout with and without access to FW, although more samplings would have been required to detect such a difference. I found one large and significant difference in diet composition - the proportion of trout with chironomid larvae in their guts was 30% in FW sections in early winter, but 58% in control sections. In autumn, 52 – 72% of all trout ingested chironomid larvae, with no difference due to FW access. This could indicate that chironomid larvae were depleted from the FW bundles during the study period, which potentially could reduce growth of trout sheltering in FW bundles. Chironomid larvae were one of the two most common prey types ingested, and also the most common invertebrate found on FW and bottom gravel during autumn.

Future research should explore the effects of fish personality and social status on sheltering behaviour, as well as on the trade-off between sheltering and foraging. Also, salmonids are well studied as predators, but not as much studied as prey (but see Harvey & Nakamoto, 2013). Salmonid sheltering behaviour as an antipredator response should be further explored by testing fish in the presence and absence of different predators, i.e. both terrestrial and aquatic, and both ecto- and endothermic predators. There is also a need for systematic studies on salmonids of different species and in different ontogenetic stages, and their behavioural response to differently sized and shaped sheltering structures, e.g. FW, LW, boulders, cobbles, streambed and aquatic vegetation. Moreover, studies of shelter use by

salmonids at low water temperatures are needed to disentangle species- and size-specific responses to shelter access during winter.

Salmonid populations are presently declining world-wide due to land-use changes, over-fishing and aquaculture (Parrish *et al.*, 1998), and habitat loss has far-reaching effects on fish (Miller, Williams & Williams, 1989) and stream-living invertebrates (Negishi, Inoue & Nunokawa, 2002). Changes in land-use may lead to interrupted pathways of material and energy between the riparian zone and the stream, and may ultimately result in loss of important microhabitats in the stream, such as loss of suitable sheltering structures. My results indicate that juvenile brown trout use sheltering structures extensively, and that the possibility to shelter may be more important than the possibility to achieve maximal growth rates for these fish during their first autumn and early winter. Also, my results suggest that an increased availability of instream structures can increase prey availability for stream-living fish, at least locally in the short-term. Taken together, this thesis supports the hypothesis that availability of sheltering structures may have far-reaching effects on survival and growth of lotic organisms. Also, my findings indicate that knowledge about the ecological role of instream structures for different lotic taxa is needed to improve conservation, restoration and management of stream ecosystems in boreal areas.

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Populärvetenskapling sammanfattning - En fisk behöver också en kvist att sitta på

En tidigare version av denna text publicerades i Forskning och Framsteg nr 5/2016.

Ris och kvistar är en viktig del av ekosystemet i våra skogsbäckar. Rishögar ökar både överlevnadschansen och mängden mat för små öringar. På senare år har vi människor börjat använda allt mer ris och kvistar som biobränsle. Vad händer då med öringen?

Det är få fiskarter som klarar att leva i de minsta skogsbäckarna. Märkligt nog hör öringen till dem, trots att den är mer känd som en stor havsfisk. Det finns stammar av små, bruna öringar som inte blir längre än 30 cm, som lever från kläckning till död i oansenliga bäckar. Allt de behöver måste finnas på plats. Om en enda livsnödvändig förutsättning försvinner från bäcken kan det betyda slutet för öringarna. Det beror på att de ofta inte har någon annanstans att ta vägen. Deras bäck slutar kanske vid en fördämning eller ett vattenfall som öringarna inte tar sig förbi. Öringen är också viktig för flodpärlmusslan, som sitter nedborrad i botten och ibland gömmer stora skimrande pärlor i sitt inre. Den kan bli över 250 år gammal, och kan bara fortplanta sig där det finns öring. Flodpärlmusslans larver lever nämligen som parasiter på öringens gälar. Trots att pärlfiske numera är förbjudet i Sverige är flodpärlmusslan starkt hotad.

I öringens känsliga ekosystem har det funnits död ved lika länge som det vuxit skog längs bäcken. Faktum är att i en helt orörd skog kan bäckarna vara fullkomligt täckta av ris, pinnar, kvistar, grenar och hela träd. Vattenytan syns inte över huvud taget, man hör bara ett svagt porlande långt nere under bråten. Det är svårt att föreställa sig en sådan skogsbäck, som mer liknar en sorts hög av spretigt skräp. Att det känns så främmande för oss visar med tydlighet hur mycket vi förändrat öringens naturliga miljö. Sådana bäckar finns inte längre kvar någonstans i Skandinavien. För att hitta dem nu för tiden måste man resa till avlägsna platser i den ryska taigan.

I min forskning studerar jag öringar under deras första levnadsår, och vad död ved betyder för dem. Det första levnadsåret är en svår period, då många öringar blir uppätta eller svälter ihjäl. Tillgången till död ved kan vara extra viktig just då. Jag har valt att studera klen ved (ris

och kvistar), eftersom små fiskar väljer att gömma sig där hellre än bland grövre grenar och stammar. Mina resultat visar bland annat att den döda veden används som gömställe i hög utsträckning av de unga öringarna, troligen för att de på så vis kan öka chansen att överleva attacker från rovdjur. Minkar, som är skickliga rovdjur, kan närapå tömma en bäck på öring – men bara om bäcken saknar gömställen såsom död ved. Detta har varit känt länge, men min forskning tyder på att öringarna dessutom väljer sina gömställen beroende på vilket sorts rovdjur som hotar dem. Det är ett av många exempel på att fiskar är mycket mer anpassningsbara och flexibla än vad man tidigare trott. En rishög är ett snabbt tillgängligt skyddsrum för en liten öring om en mink plötsligt dyker upp. Om det är vinter och kallt i vattnet, så föredrar många små öringar att gräva ner sig bland stenarna på bäckens botten. Man tror att detta ger dem ännu bättre skydd mot mink och andra varmblodiga rovdjur, som är mycket snabbare på vintern än vad fiskar är. Frågan är vad som händer om en kallblodig rovfisk finns i närheten? Gräver öringarna ner sig extra mycket även då? Jag och en kollega undersökte detta genom att fånga vilda lakar och öringar och studera dem i konstgjorda bäckar inomhus. Lakar äter gärna öring, och de är duktiga grävare som dessutom har möjlighet att känna lukten av en nedgrävd öring. Vår forskning visade mycket riktigt att öringarna gräver ner sig mer sällan då laken finns i närheten. Däremot använde de död ved som gömställe om de hade möjlighet, lika ofta oavsett om lake fanns i närheten eller ej. Det är lätt att tänka sig att en liten fisk kan manövrera smidigt i labyrinten av kvistar och ris, medan en större fisk eller en mink inte ens kan stänga sig in i bråten. Men död ved ger inte bara skydd utan är också ett skafferi.

Öringen äter förstås inte trä, utan sambandet är mer komplicerat än så. De små, bäcklevande öringarna lever nästan enbart på insektslarver – sådana som ska kläckas till nattsländor, dagsländor, bäcksländor, trollsländor, knott och mygg. De kompletterar denna föda med daggmaskar, iglar och snäckor. Många av dessa småkryp lever i sin tur på växtmaterial som flyter med strömmen. Vissa äter av hela löv, vissa lever på detritus, som mest består av nedbrutna växter. Andra lever på biofilm, ett slemmigt lager av alger, svampar och bakterier som täcker allt som får ligga i vatten ett tag. De kryp som filtrerar detritus ur vattnet behöver sätta fast sig själva på en yta där vattnet strömmar förbi. Ved är en alldeles utmärkt yta både för dem

och för biofilmen, och ju mer ved, desto större yta, jämfört med enbart en slät botten av sand eller grus. Ris och kvistar kan också fånga upp hela sjok av flytande löv. Död ved kan alltså bli ett slags skafferi åt öringen, genom att förse öringens bytesdjur med mat. I en av mina studier såg jag mycket riktigt att det fanns extra många bytesdjur i vattenmassan nedströms knippen av ris. Död ved ökar alltså antalet bytesdjur, åtminstone lokalt. Betyder det att öringen äter mer och växer fortare bland ris och kvistar? Nej, åtminstone inte alltid, visade det sig i ett försök som jag gjorde i konstgjorda bäckar utomhus. De öringar som hade möjlighet att gömma sig i risknippen växte långsammare än dem som saknade den möjligheten. Att ha låg tillväxt är i allmänhet inte bra för en fisk, eftersom högre tillväxt brukar öka chansen att få stor och framgångsrik avkomma. Något extraordinärt måste ofta till för att en fisk ska åsidosätta sin tillväxt. I det här fallet fanns det troligen en risk att bli uppäten för de fiskar som inte gömde sig. Efter att försöket avslutades visade det sig av en slump att öringarna tolkat situationen rätt. Tre minkar hittade ett hål i stängslet runt försöksanläggningen, och gjorde snabbt slut på mer än två tredjedelar av öringarna som saknade gömställen, men åt bara upp knappt hälften av öringarna som kunde gömma sig i risknippen.

Hur ser framtiden ut för öringen i våra skogsbäckar? Det avgör vi människor. Situationen är ovanligt sammansatt när det gäller öringen, eftersom öringens behov av kallt vatten och död ved kräver olika insatser av oss. För att ge en kort sammanfattning av dilemmat: Den globala uppvärmningen är ett stort hot mot öring, som dör om vattentemperaturen är 25 grader i en vecka eller mer. Öringens rom är ännu känsligare – den förstörs om vattnet är varmare än 13 grader. Eftersom många öringar är instängda i sina bäckar så räcker det med en kort period av för varmt vatten för att de ska dö ut – och eventuella flodpärlmusslor med dem. Å andra sidan kan vi inte utan vidare plocka ut allt biobränsle som finns i skogen för att göra klimatsmartare bränsle - för biobränsle är ofta just detsamma som öringarnas klena döda ved, som hjälper dem att överleva sitt första år. Vid avverkningar är det därför viktigt att lämna en rejäl skyddszon av träd och buskar längs bäckkanten. Då kan ny död ved falla ner i bäcken i takt med att den gamla spolats bort. På så vis ges en tidsfrist att samla mer kunskap om varför fisken behöver död ved – utan att vi utrotar fisken i våra bäckar under tiden.

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Fine stream wood. Effects on drift and brown trout

Stream ecosystems and their riparian zones have previously been regarded as two different ecosystems, linked through numerous reciprocal subsidies. Today, ecologists agree that the stream and the riparian zone should be regarded as one system, the stream-riparian ecosystem, which is characterised largely by the subsidies between land and water. In this doctoral thesis, I explore one such subsidy – the input of fine stream wood (FW) to streams. Wild stream-living young-of-the-year brown trout (*Salmo trutta*) was chosen as study species. My results show that the local density of drifting prey is higher in the presence of FW than in its absence, and that young-of-the-year brown trout decrease their diurnal foraging time and prey capture success when FW is added to their habitat. I show that trout decrease their activity in the presence of FW, aggregate in FW bundles, and have lower growth rates than trout without FW access. Taken together, my results indicate that young-of-the-year brown trout spend considerable amounts of time in FW bundles, and by doing so they miss the opportunity for higher growth and foraging rates outside of the shelter. The most probable explanation for this behaviour is that growth is traded off against survival.

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