



Effects of fine woody debris on juvenile brown trout (*Salmo trutta*) and drifting invertebrates

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Biology

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Licentiate thesis

Abstract

In boreal forest streams, invertebrates and fish such as brown trout (*Salmo trutta*) are known to benefit from in-stream wood. The studies presented in this thesis explore how drifting stream invertebrates respond to addition of fine woody debris (FWD), and how young-of-the-year brown trout behave in habitats with and without FWD. The first paper reports results from a field experiment, where I added FWD to seven localities in four streams, and measured its effect on the drift density, biomass and taxon diversity of invertebrate drift. Drift was measured upstream (control) and downstream of FWD bundles every second week on five occasions from June to August. After 8-10 weeks the density, biomass and taxon diversity were higher downstream of the FWD than immediately upstream (controls). In the second paper, I describe effects of FWD on 0+ brown trout in laboratory stream channels. In-stream structure is known to affect salmonid behaviour, but few studies have explored the effect of fine wood on 0+ trout behaviour. I studied trout alone and in groups of four at three FWD densities: no FWD, intermediate levels and high levels. The time spent cruising by trout was lower when densities of FWD were high than when FWD was absent. Cruising time was also higher when trout were in groups than when alone. The proportion of time spent for successful prey attacks was higher when FWD was absent than when there was an intermediate level, but it was not affected by the number of fish in the channel. In addition, more time was spent sheltering at the high densities of FWD than at intermediate densities. The results suggest that FWD affects the behaviour of juvenile trout. The fish respond to FWD by decreasing their swimming costs and thereby their energy expenditures, but since foraging also decreases, it is unclear whether or not their average net energy gain increases or decreases.

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List of papers

This thesis is based on the following two papers, which are referred to by their Roman numerals.

- I. Enefalk, Å. and Bergman, E. (2014). Effects of fine wood addition on macroinvertebrate drift in boreal forest streams. *Manuscript*.
- II. Enefalk, Å. and Bergman, E. (2014). Juvenile brown trout response to fine woody debris in experimental stream channels. *Manuscript*.

Contributions

Åsa Enefalk and Eva Bergman contributed equally to the development of the basic ideas and concepts and the study design. Åsa Enefalk performed the field and laboratory work, collected the data, ran the statistical tests, and wrote both of the papers. Eva Bergman provided statistical advice and made valuable comments for improving both of the papers.

Introduction

Small forest streams are tightly linked to their riparian zones. Stream biota benefits from terrestrial inputs of leaves, needles and invertebrates. Also, woody debris that enters from the riparian zone is an important habitat feature for aquatic insect larvae and salmonids in boreal forest streams (Fig. 1). It provides a substrate for invertebrate attachment and feeding (Benke et al. 1985), and a refuge from predation and current for invertebrates (Dudley and Anderson 1982, Drury and Kelso 2000) and salmonids (Fausch 1984 and 1993, Hughes and Dill 1990). Woody debris (WD) can increase benthic and drift density, biomass and diversity of invertebrates (Gerhard and Reich 2000, Hernandez, Merritt and Wipfli 2005, Lester, Wright and Jones-Lennon 2007, but see Liljaniemi et al. 2002 and Testa, Douglas Shields and Cooper 2011). In-stream large woody debris (LWD) is related to higher biomass, abundance and survival of 1+ and older salmonids (Fausch and Northcote 1992, Quinn and Peterson 1996, Antón et al. 2011, Langford, Langford and Hawkins 2012).



Fig. 1. In-stream wood is a key feature of invertebrate and brown trout habitat in small boreal forest streams. River Tvärån has earlier been cleared from debris, but wood is continuously entering the stream from the riparian zone. Photo A. Tedeholm.

However, salmonid response to WD is dependent on the species and the ontogenetic stage of the fish (Keith et al. 1998, Langford et al. 2012), and also on the size of the WD. For example, salmonid fry density and biomass can increase in stream reaches with added fine woody debris (FWD; Culp, Scrimgeour and Townsend 1996) whereas LWD is avoided by 0+ brown trout, but used as cover by 1+ trout and older (Langford et al. 2012).

Effects of WD on stream invertebrate drift

In-stream woody debris will increase the retention of nutrients and litter (Dolloff 1993, Smock,

Metzler and Gladden 1989) and increase variation in structure and flow pattern (Bilby and Ward 1989). Woody debris that falls into streams will generally be covered by biofilm and colonized by aquatic macroinvertebrates in 1-8 weeks (Couch and Meyer 1992, Nilsen and Larimore 1973, Drury and Kelso 2000,

Bond et al. 2006). Thereafter, the invertebrate community will be relatively stable, and density and biomass of drifting invertebrates downstream of WD will increase (Sagar and Glova 1992), due to e.g. food shortage and escape from colonizing predatory invertebrates (Elliott 1968, Malmqvist and Sjöström 1987, Brittain and Eikeland 1988). Also, invertebrate biodiversity can increase when WD is reintroduced to streams (Johnson, Breneman and Richards 2003, Lester et al. 2007, Lester and Boulton 2008). Most research on WD effects on stream invertebrates has been focused on LWD (but see Lester and Wright 2009), partly because it is more long-lived in stream ecosystems than FWD is. However, even small pieces of wood will provide a potential substrate area for invertebrates (O'Connor 1991, Hoffmann and Hering 2000), and in small streams, FWD may be an important part of the total WD load (Triska and Cromack 1980). Also, FWD can create a more variable flow pattern than LWD, and thereby offer a more complex habitat to invertebrates (Wallace, Grubaugh and Whiles 1996, Collier and Bowman 2003). This may affect both the density and diversity of the invertebrate fauna.

Effects of WD on juvenile brown trout

Brown trout respond to woody debris in many ways. WD can act as overhead cover, and as such a shelter from avian and mammalian predators. Also, it can provide in-stream shelter from predatory fish. The mere presence of sheltering structures has been shown to lower metabolism of salmonids (Millidine, Armstrong and Metcalfe 2006). WD can also act as a current refuge, but water velocity need to be relatively high before salmonids seek refuge from it (Jonsson and Jonsson 2011) and swimming costs are often not crucial for salmonid performance (Hughes and Dill 1990). By lowering the visibility, WD acts as a shelter from aggressive conspecific salmonids (Sundbaum and Näslund 1998, Imre, Grant and Keeley 2002). This can decrease aggressiveness, and thereby energy expenditure. Poor visibility due to WD can however have negative consequences for salmonid foraging. As salmonids are visual predators, it is possible that in-stream structure can hinder their foraging after a threshold level of structure is reached, as reported for the predatory largemouth bass (Gotceitas and Colgan 1989). Moreover, reduced visibility can reduce the size of feeding territories, making it more energetically costly to defend them (Wilzbach, Cummins and Hall 1986, Eason and Stamps 1992, Venter et al. 2008). Also, in-stream structures such as boulders and WD may both enhance (Finstad et al. 2007) and decrease (Teichert et al. 2010) growth of salmonids. This may partly be due to the different behavioural responses of different-sized fish. It is reasonable to assume that small young-of-the-year trout will respond

differently to large vs small in-stream structures. LWD and FWD are probably not viewed as similar habitat components by small trout.

In-stream WD can affect drift-feeding by juvenile brown trout

Brown trout are highly specialized to use drifting invertebrates as prey (Elliott 1994, Sagar and Glova 1992), although trout in some populations feed epibenthically (Kreivi et al. 1999). An increase in habitat quality, e.g. an addition of WD, will provide benefits to invertebrates and thus also potential prey for trout. Prey density has a significant effect on abundance of predatory fish, and positive habitat effects are often mediated by positive effects of the habitat on prey density (Lehtinen, Mundahl and Madejczyk 1997, Grant et al. 1998, Keeley and Grant 2001, Imre et al. 2002, Urabe et al. 2010). This is consistent with the foraging model suggested by Kawai et al. (2014). According to this model, salmonid biomass in streams is related to both cover ratio and mean net energy intake (NEI) of the fish. The NEI, in turn, is related to capture area of the foraging fish, velocity at foraging point, drift biomass and swimming costs.

Newly introduced FWD seems to mainly increase the drift of small invertebrates, maybe because oviposition on wood is a common way of colonizing it. This will probably lead to a high density of newly hatched small individuals, and high benthic densities of invertebrates will increase their propensity to drift (Brittain and Eikeland 1988, Spänhoff et al. 2006). This drift of small animals can provide important food items to the smallest-sized brown trout. In addition, wood will attract the same invertebrate taxa that many populations of brown trout feed on (e.g. *Baetis* and Simuliidae; Rader 1997, Dudley and Anderson 1982, Kimbirauskas et al. 2008). Taken together, this may mean that invertebrate drift from FWD is an important food source especially for young, gape-limited trout.

Objectives

The main objective of this thesis was to study the effect of FWD in small boreal forest streams on drifting invertebrates and young-of-the-year brown trout behaviour. First, I performed a field experiment, where my main interest was to shed light on potential effects of FWD on abundance, biomass and diversity of aquatic invertebrate drift. The objective of the second, laboratory study was to explore juvenile brown trout behavioural response to different densities of FWD. In particular, I was interested in potential effects of FWD and trout density on trout foraging, aggressiveness, sheltering, and swimming.

Materials and methods

One of the studies in this thesis was conducted in the field from June to August 2011 (Paper I), whereas the other study was conducted in the aquarium facility at Karlstad University during September-December 2012 (Paper II).

For the field experiment of Paper I, birch branch bundles (*Betula pubescens*) were placed in natural streams at seven sites in three catchments. Each bundle consisted of 20 branches, c. 1.3 m long, with a FWD volume per bundle of c. 8 dm³. By measuring drift up- and downstream of each bundle, I could directly test the effect of FWD on drift, as the upstream bundle acted as a control for that site. Drift was sampled every second week on five occasions from mid-June to mid-August, starting two weeks after the introduction of FWD. I used 500-micrometer-mesh drift nets with a 30x40 cm mouth opening and a length of 99 cm (Wildco™). One drift net was set 1-10 m upstream of the FWD bundle at each site, and the other 1-2 m downstream of the bundle. At each sampling, water velocity was measured with an Owen's hydropropeller at the mouth of each drift net, half-way from the lower drift net frame to the water surface. After 24 hours of sampling, I brought the drift samples to the laboratory, sorted invertebrates from debris, measured wet mass, and preserved invertebrates in 70% ethanol. Later, I counted the number of invertebrates per sample, identified their taxa, and measured the length of each individual. Data were then analysed for drift density, wet mass, and taxon diversity using a Shannon-Wiener index. Dry mass was calculated from length-weight-regressions (unpublished data).



Fig. 2. In the trial of Paper II, three FWD habitats were created in laboratory stream channels. This is the upstream part of the channel with high FWD density, viewed from above. Water flows towards the photographer through the meshed fence in the upper left corner of the photograph.
Photo Å. Enefalk.

session, where one red chironomid larva was released through a feeding tube every 15th second, until a total of ten larvae were released.

Video recordings were used to determine the amount of time spent (1) swimming, (2) cruising (swimming with speeds of 0.5-2 fish lengths/second), 3) attacking drifting prey, (4) making aggressive attacks, (5) hiding in or underneath the FWD, and to determine (6) the number of prey taken and (7) the number of aggressive attacks and (8) identify the fish by the VIE-mark.

For the laboratory experiment (Paper II), I used 39 juvenile brown trout (fork length 45-65 mm), collected by electrofishing in River Tvärån. All fish were VIE-marked alongside the anal fin (*sensu* Olsen and Vøllestad 2001). During trials, the fish were filmed in the presence and absence of conspecifics at three densities of FWD in a 0.95x1.85 m section of a 7-m-long stream channel. Water temperature was held at 13° C and depth at 25 cm. Water velocity was zero <5 cm above the bottom gravel and in the FWD, and 9-25 cm/s at 60% of the depth. FWD was placed parallel to the stream direction, so that half of the bottom area was covered by FWD (Fig. 2). Three FWD densities were used: 0, 1.2 and 9 dm³/m² bottom area. Fish were observed alone and together with three conspecifics. Trials were conducted during the morning hours. Each trial consisted of 5 minutes of video recording, beginning with a 2.5 minute feeding

Summary of results

In Paper I, there were large differences in invertebrate drift density and biomass between sites. Nevertheless, the general pattern was that drift density and biomass peaked in mid-July and reached a minimum in mid-August. In sites with FWD, there was no minimum in mid-August; instead there was a small increase. A *t*-test showed that the average drift density and biomass were higher downstream of the FWD bundles than in the upstream control in mid-August, some 8-10 weeks after FWD was added (Fig. 3 and 4). This was also true for taxon diversity as measured by Shannon-Wiener index and analyzed by a Wilcoxon related test.

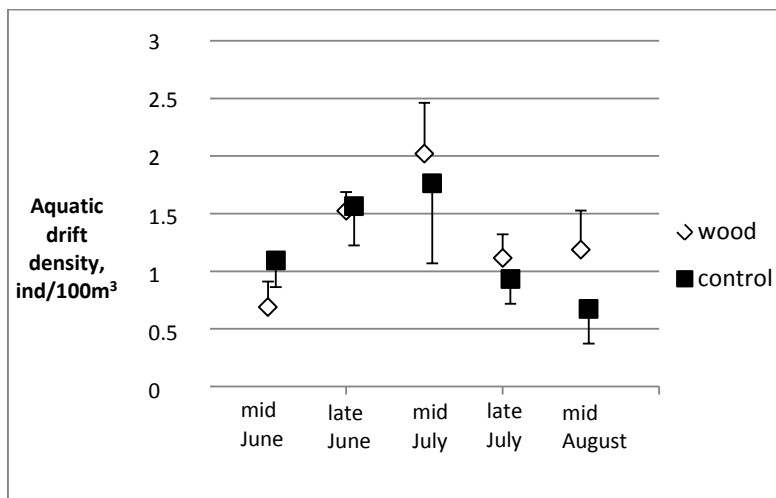


Fig. 3. Mean aquatic drift density (number of individuals/100 m³ ± 1 SE) in FWD and control treatments during the entire season. Data for all aquatic taxa are pooled. Aquatic drift density is square root transformed.

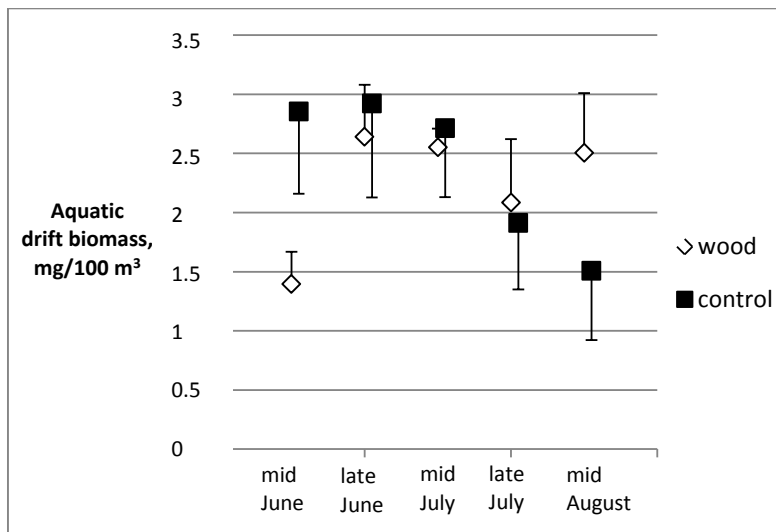


Fig. 4. Mean aquatic drift biomass (wet mass/100 m³ ± 1 SE) in FWD and control treatments during the entire season. Data for all aquatic taxa are pooled. Aquatic drift biomass is square root transformed.

In paper II, I found a number of behavioural differences related to the density of FWD. Trout spent a large proportion of their time sheltering in the wood, and this proportion was larger in the high than in the intermediate FWD habitat (Fig. 5 a). When it concerns swimming behaviour, the proportion of time spent cruising was generally low regardless of treatment (Fig. 5 b). Nevertheless, in the absence of FWD, trout spent more time cruising than when FWD was present, and they also cruised more in the four fish groups than when alone. When it concerns foraging, the time spent on successful prey attacks was lower at intermediate densities of FWD than in the absence of FWD (Fig. 5 c). There was no main effect of FWD density on aggressiveness.

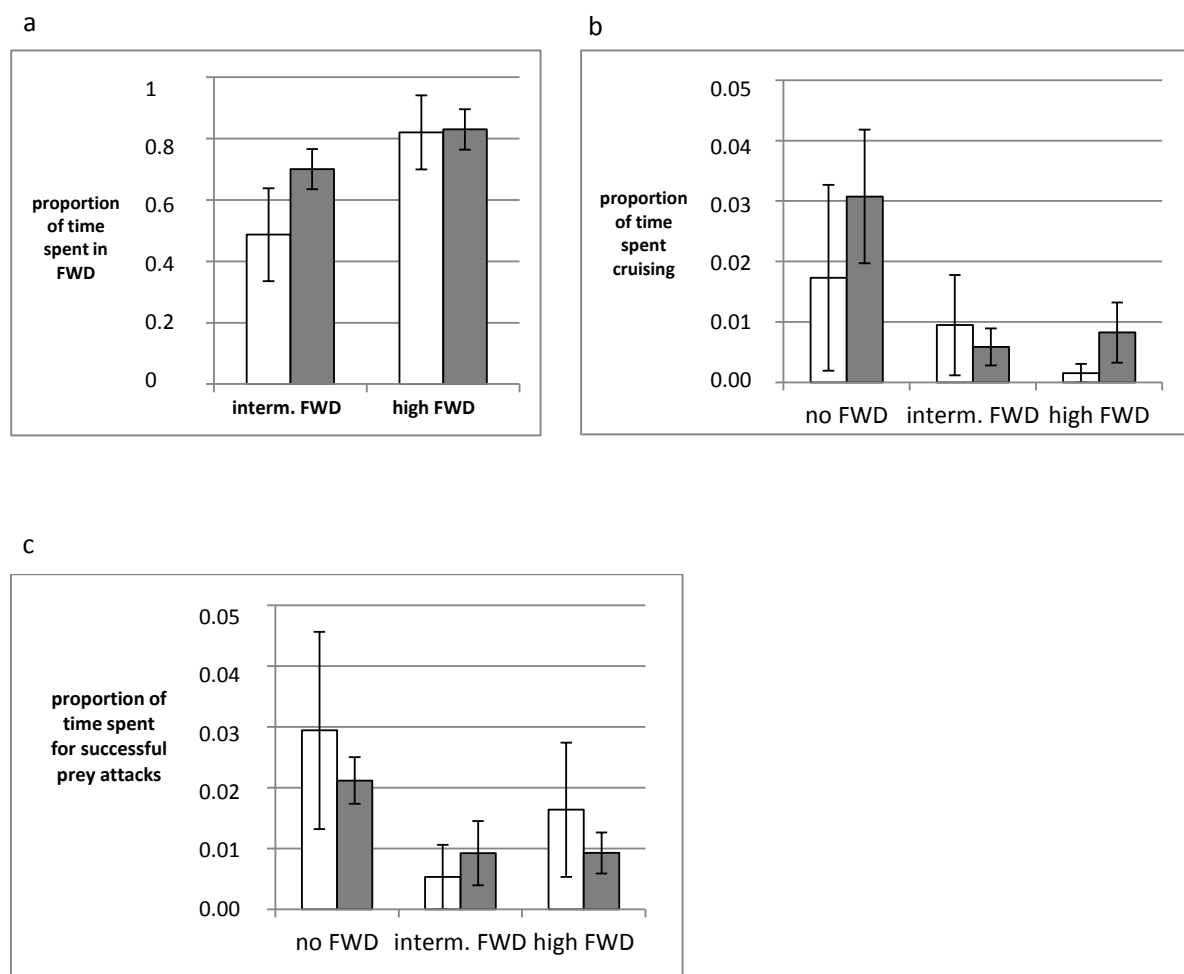


Fig. 5. Proportion of time (mean \pm s.e.) spent a) sheltering in FWD, b) cruising and c) on successful prey attacks, for single fish (open bars, $n = 11$) and four-fish groups (filled bars, $n = 9$).

In the field study (Paper I) the mid-August invertebrate drift downstream of the FWD was higher than the drift upstream of the FWD. As this should mean an increased food subsidy for brown trout, I roughly assessed the ecological impact of this food subsidy by applying the foraging model proposed by Kawai et al. (2014). I did this by combining mid-August data from Paper I on average drift dry mass in FWD and control sites, and data from the laboratory experiment (Paper II) on water velocities, average fish weights, capture areas and cover. For energy content of the prey, I used data from Cummins and Wuycheck (1971). With this approach, the prey density sampled by an average drift net downstream of a FWD bundle could support a salmonid biomass 2.2 times larger than the prey density at the control site. However, this calculation was based on the assumption that there was no overhead cover in the stream. If I assume that the FWD bundle added a 50% overhead cover, whereas the cover ratio of the control site was zero, estimated salmonid biomass in FWD sites were 2.5 times greater than in control sites.

Discussion

The objective of this thesis was to investigate the effect of FWD on drifting stream invertebrates (Paper I) and on a drift-feeding fish - brown trout (Paper II). Paper I explores the relationship between the addition of FWD and invertebrate drift density, biomass and diversity. These relations have, to my knowledge, rarely been studied and never in Scandinavia. Paper II contributes to the rather limited body of literature on how fish use FWD and how it affects their behaviour.

As ecological studies on in-stream wood have focused mostly on LWD, I wanted to explore the role of FWD and compare it to our current understanding of LWD in stream ecosystems. Studies of FWD have increased in relevance in today's society, as FWD, which was earlier left in managed forest ecosystems, is now being harvested for biofuel (Nordén et al. 2004). Also, the management of brown trout streams has mainly been concentrated upon creation of better spawning areas, building of fish passages, and addition of large structures such as LWD and boulders (Jonsson and Jonsson 2011). These management efforts have largely benefitted large-sized individuals (Jonsson and Jonsson 2011). For small trout in their first year of life, such measures will have little effect. Measures to increase the density of FWD, on the other hand, are expected to benefit small trout (Culp et al. 1996, Langford et al. 2012). In addition, traditional management of brown trout streams has often been performed without considering the effect on stream invertebrates (Muotka and Syrjänen 2007). Invertebrates are benefitted by FWD (Lester and Boulton 2008)

and by aquatic mosses (e.g. Frost 1942), a habitat component that often decreases when conventional stream restoration takes place (Muotka and Syrjänen 2007). The different needs of stream invertebrates, juvenile and older brown trout indicate that managing these systems may be difficult, and moreover, that more knowledge about the role of FWD is needed.

I suggest that small trout respond in different ways to FWD and LWD. In Paper II, the results differ from earlier research on LWD and small brown trout (Gustafsson, Greenberg and Bergman 2012). Small trout in their study did not reside on the bottom, but higher up in the water volume, whereas large trout were bottom-dwelling. Small trout did not experience difficulties in foraging in LWD habitats, but large trout did (Gustafsson et al. 2012). In contrast, in the habitats with FWD (Paper II), the small young-of-the-year trout were bottom-dwelling and foraged less in the presence of FWD than in its absence. Also, the fish spent considerably less time cruising (1.2%) in Paper II than in Gustafsson et al. (2012), where small trout averaged 27.2%, which is similar to the total time spent for all kinds of activity by the trout in the absence of FWD (Paper II). However, the small *single* fish in Gustafsson et al. (2012) swam on average 35% of their time in the *absence* of LWD, compared to an average of 3.5% for single fish in the absence of FWD (Paper II). This large difference is probably not caused by different responses to LWD and FWD, but has several other possible explanations. Trout in the LWD study were kept separately, whereas trout in the FWD study were familiar with each other. Familiar fish are known to fight less than unfamiliar ones, and instead focus on predator vigilance and foraging (Griffiths et al. 2004). Also, small trout in the LWD study may have been affected by the trials where they met unfamiliar, larger trout.

I propose that in natural streams, the FWD effects on trout behaviour observed in the laboratory (Paper II) are accompanied by increased prey availability to trout. The FWD in my field study (Paper I) increased the biomass of drifting invertebrates by approximately 2 mg dry mass per 24 hours, assuming that the drift nets received the entire drift biomass originating from the FWD. This corresponds to c. 16% of a common daily ration of one young-of-the-year trout (Elliott 1975). The timing of this potential food subsidy may enhance the importance of it, as the increase in FWD-affected drift was recorded in late summer (Paper I), when drifting food is generally scarce (Leeseberg and Keeley 2014) and when the need for growth is high (Jonsson and Jonsson 2011). However, more studies are needed to determine if this increase occurs in late summer regardless of when the FWD entered the stream, or if it occurs when a certain time has passed since FWD colonization began. In addition, prey availability has been reported to interact with access to cover in determining the

biomass of stream salmonids, e.g. in the foraging model suggested by Kawai et al. (2014). Using this model to estimate the impact of the FWD addition on potential trout biomass showed a 2.2-fold increase. If the potential difference in cover between sites with and without FWD was considered, the potential trout biomass in FWD sites was 2.5 times greater than the biomass in control sites. Thus, most of this difference in fish biomass was explained by the greater biomass of prey at FWD sites, and less by the cover. Also, the laboratory experiment indicated that young-of-the-year trout can benefit energetically from FWD, as the presence of FWD decreased the average time cruising by 27% (Paper II). Taken together, the food subsidy, the access to cover and the decreased activity level imply that FWD has positive effects on juvenile brown trout energetics. However, most trout in my study used FWD for sheltering rather than foraged outside the FWD. This may have been due to that foraging was difficult in the FWD habitat, as FWD limited the visibility of prey for trout, and thereby lowered the encounter rate (Wilzbach et al. 1986, Gotceitas and Colgan 1989, O'Brien and Showalter 1993). It may also be due to a trade-off between sheltering and foraging, where the trout preferred to shelter. This could imply that trout do not always use the food subsidy provided by FWD, but instead choose to use FWD as for example a predatory refuge. If this is the case, the trade-off between survival (predatory refuge) and energy intake (foraging) should benefit survival rather than growth. This can however be counteracted if the sheltering trout feed on epibenthos instead of drift, as has been proposed for some trout populations (Kreivi et al. 1999). Sheltering could also provide a growth benefit if it reduces swimming costs. However, I judge that this was not the case in my study (Paper II), as water velocity was zero near the bottom outside the FWD, and moreover, swimming costs have been judged less important than energy intake for the overall energetics of salmonids, at least when prey abundance is high (Hughes and Dill 1990). Moreover, the choice to shelter instead of forage may lead to high densities of trout in the sheltering structure, and thereby explain the low growth in high-structure habitats as reported in studies of e.g. Teichert et al. (2010).

An important question is if stream size will affect the ecological impact of in-stream FWD. In the field study of Paper I, stream invertebrate drift density varied extensively between different streams. Although not tested, the magnitude of the drift density appeared to be related to stream size and catchment area. Of the four streams studied, two were c. 1.5 m wide with average drift densities of 3 and 5 mg wet weight/100 m³ respectively, while two were c. 3.5 m wide with average drift densities of 9 and 12 mg wet weight/100 m³ respectively (data from all samplings June-August). This is consistent with

results reported by others, e.g. the lower drift abundance of small tributaries compared to that of main-stem rivers (Leeseberg and Keeley 2014). Coincidentally, small streams do not only exhibit low drift densities, but also higher retention of LWD and FWD than larger streams (Seo, Nakamura and Chun 2010). In small forest streams, the presence of FWD may mitigate the harsh conditions for stream invertebrates by retaining organic matter and offering shelter from current, and thereby enhance benthic and drift density to a somewhat higher level. I speculate that this may mean a significant food subsidy for trout. Resident trout in such streams may never grow large, as prey abundance will be too low and stream size too small to allow extensive foraging of large fish (Rosenfeld and Taylor 2009). Still, the presence of FWD in small streams may be important for resident trout populations, and also, it may enhance rearing habitats for migrating trout. When planning future research and management of trout in small streams, it may be fruitful to consider these couplings of stream size, FWD, invertebrates and trout.

In summary, my results show that in-stream FWD can increase the amount and diversity of drifting invertebrates and affect the behaviour of juvenile brown trout. The positive relation between FWD and drifting invertebrates suggests that FWD increases the carrying capacity of the habitat. Brown trout may benefit from FWD by behaviour-mediated changes in energetics, such as decreased swimming and increased sheltering, and in natural streams probably also by the increased density of drifting prey.

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Effects of fine woody debris on juvenile brown trout (*Salmo trutta*) and drifting invertebrates

In boreal forest streams, woody debris is an important habitat component. Stream invertebrates and salmonids such as brown trout benefit from in-stream wood. The studies presented in this thesis explore how drifting stream invertebrates respond to addition of fine woody debris, and how young-of-the-year (0+) brown trout behave in habitats with and without fine woody debris. The first paper reports results from a field experiment where fine woody debris was added to streams, and invertebrate drift was measured in order to detect impacts of the fine woody debris on drift density, biomass and taxon diversity. In the end of the season, the fine woody debris-affected drift samples showed higher density, biomass and taxon diversity than the control samples. In the second paper, I describe effects of fine woody debris on 0+ brown trout, studied in laboratory stream channels. Trout were tested in habitats without fine woody debris, with an intermediate fine woody debris density, and with a high fine woody debris density. Swimming activity and foraging time were significantly lower when fine woody debris was present than when it was absent. More time was spent sheltering at the high fine woody debris density than at the intermediate one. The increasing exploitation of fine woody debris for biofuel purposes should be considered in relation to the effects on brown trout and stream invertebrate habitat.

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