

Effect of fine wood on juvenile brown trout behaviour in experimental stream channels

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Abstract – In-stream wood can increase shelter availability and prey abundance for stream-living fish such as brown trout, *Salmo trutta*, but the input of wood to streams has decreased in recent years due to harvesting of riparian vegetation. During the last decades, fine wood (FW) has been increasingly used for biofuel, and the input of FW to streams may therefore decrease. Although effects of in-stream FW have not been studied as extensively as those of large wood (LW), it is probably important as shelter for small-sized trout. In a laboratory stream experiment, we tested the behavioural response of young-of-the-year wild brown trout to three densities of FW, with trout tested alone and in groups of four. Video recordings were used to measure the proportion of time allocated to sheltering, cruising and foraging, as well as the number of aggressive interactions and prey attacks. Cruising activity increased with decreasing FW density and was higher in the four-fish groups than when fish were alone. Foraging decreased and time spent sheltering in FW increased with increasing FW density. Our study shows that juvenile trout activity is higher in higher fish densities and that trout response to FW is related to FW density and differs from the response to LW as reported by others.

Key words: salmonid; YOY; streams; wood; small woody debris

Introduction

Forest streams are intimately linked to their surrounding landscapes in a number of ways, and one such linkage is the wood that enters streams from the riparian zone. In the streams, wood can increase the retention of nutrients and matter (Bilby & Ward 1989; Smock et al. 1989; Muotka & Laasonen 2002) and modify the physical habitat by changing depth and current velocity (Riley & Fausch 1995; Keim et al. 2002), as well as provide a substrate for macroinvertebrates (Benke et al. 1985; Lester et al. 2007).

Salmonid densities are often positively correlated with occurrence of wood, and therefore, salmonids are generally considered to benefit from high densities of wood that adds a structural habitat component (Angermeier & Karr 1984; Fausch & Northcote 1992; Sweka & Hartman 2006; White et al. 2011; Langford et al. 2012). For example, wood is known to provide shelter from currents and predators (Werner et al. 1983), to decrease visibility and reduce

activity and aggression in territorial salmonid species (Kalleberg 1958; Sundbaum & Näslund 1998; Imre et al. 2002). Also, stream-living salmonids feed on macroinvertebrates which can use wood as a substrate. However, very high levels of structural complexity can reduce fish foraging efficiency (Gotceitas & Colgan 1989) by, for example, decreasing water velocity and thus the supply rate of drifting prey, and by physically impeding attacks on prey (O'Brien & Showalter 1993; Gustafsson et al. 2012). Stream wood can moreover have different effects across individual fish, for instance by supplying refuge for subordinate individuals while simultaneously conflicting with territory defence in dominants.

Salmonid responses to in-stream structure can vary due to structure characteristics and fish size (White-way et al. 2010). For instance, the presence of boulders or experimental shelters can affect energy budgets of salmon parr in a negative or positive way respectively (*Salmo salar*; Kemp et al. 2005; Millidine et al. 2006). Large stones and experimental

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plywood dividers can affect territory size, but not growth rate or population density of juvenile rainbow trout (*Oncorhynchus mykiss*; Imre et al. 2002). Moreover, salmonid responses to wood seem partly to be the result of an interplay between fish size and the dimension of the wood, as large wood (LW) attracts brown trout (*Salmo trutta*) ≥ 10 cm (Fausch & Northcote 1992; Antón et al. 2011; White et al. 2011), whereas a low abundance of small brown trout (< 7 cm) is reported for LW accumulations (Langford et al. 2012). However, small brown trout may respond to wood in a similar way as small rainbow trout, that is with higher abundances in *fine* wood (FW, < 0.1 m diameter) than in other parts of the stream (Culp et al. 1996). Large brown trout, but not small, can feed more efficiently in the presence than in the absence of LW (Gustafsson et al. 2012). However, not much is known about the effect of FW on the behaviour and performance of small salmonids.

The density of fish may have varying effects on individual performance and behaviour. Increased fish density can mean increased fish activity, often due to more aggressive interactions between individuals (Cole & Noakes 1980; Cooke et al. 2000; Gustafsson et al. 2012; but see Fenderson & Carpenter 1971). Growth and mortality rates of juvenile brown trout in streams are density dependent (Lobón-Cerviá 2007; Vøllestad & Moland Olsen 2008), and the density dependence can be more pronounced for small than large fish (Jenkins et al. 1999). Moreover, migration of salmonids has been reported to increase with increasing fish densities (Imre et al. 2005). As density-dependent effects influence salmonid ecology and behaviour, it is likely that use of wood is also density dependent. We therefore pursue the evaluation of combined effects of salmonid density and wood abundance on individual fish behaviour.

Previous studies have focused mainly on the role of in-stream LW, as forestry practices have reduced the input of LW to streams (Culp et al. 1996). The abundance of in-stream FW, on the other hand, has changed little in response to modern forestry practices (e.g. Flebbe & Dolloff 1995). However, there has been a recent increase in the rate of exploitation of FW for biofuel production (Johansson 2000; Malinen et al. 2001). As the novel use of FW as a natural resource will likely affect its abundance in streams, it is crucial to evaluate the effects of FW on stream biota to assess the potential anthropogenic impacts of this forestry practice.

As very little is known about how brown trout use FW, we conducted an experiment where we tested the effect of three densities of FW (no FW, intermediate FW and high FW) on the behavioural response

of young-of-the-year brown trout, observed alone and in groups of four during foraging in in-door laboratory streams. We hypothesised that activity, aggression and foraging would decrease with increasing FW density and that activity and time spent in FW would be higher in the four-fish groups than when fish were alone.

Material and methods

Experimental habitat

Trials were conducted in three 7-m-long in-door stream tanks, consisting of five compartments: a headbox, riffle, run, pool and filter box. Only the run compartments were used in the experiment. Each run compartment measures 0.95×1.85 m and is equipped with a glass window on one side. Water temperature and depth were maintained at 13°C and 25 cm respectively. The photoperiod was 12:12 h. Three different FW treatments, one per stream channel, were chosen to mimic conditions in streams of central Sweden. The high FW density contained 9 dm^3 of FW per m^2 bottom substrate, a density supposedly common before the use of modern forestry practices and other human interventions (Dahlström 2005 and references therein). The intermediate FW density contained 1.2 dm^3 of FW per m^2 bottom substrate, which is close to the mean value found in forested nature reserves today (Nordén et al. 2004). The no FW density represented a condition devoid of in-stream wood. All FW was birch wood (*Betula pubescens*), put in a natural stream when fresh, and conditioned there for 14 months before the experiment was started. Before the FW was put in the experimental streams, it was flushed with water under high pressure and left to dry for 1 week to remove the invertebrate fauna. The root diameter of the branches varied between 1 and 2 cm, and the length of the branches was 1.0–1.7 m. For all treatments, the substrate consisted of 25 mm gravel. The FW was placed parallel to the water flow and covered half of the bottom area (Fig. 1 a and b). In all channels, water velocity was zero close to the bottom, on both sides of the midstream area, and inside and underneath the FW in the two channels with FW. Midstream water velocity (Owen's hydropropeller) at 60% of the depth outside of the FW varied between 9 and 11 cm s^{-1} , 10 – 14 cm s^{-1} and 19 – 25 cm s^{-1} at the no, intermediate and high FW density respectively. This difference was significant (one-way ANOVA, $F_{2,9} = 42.708$, $P = 0.0001$), with higher water velocities in the high FW treatment than in the two lower ones (Scheffè's *post hoc* test, $P = 0.0001$). Trout resided only in low-velocity areas, except when attacking prey.

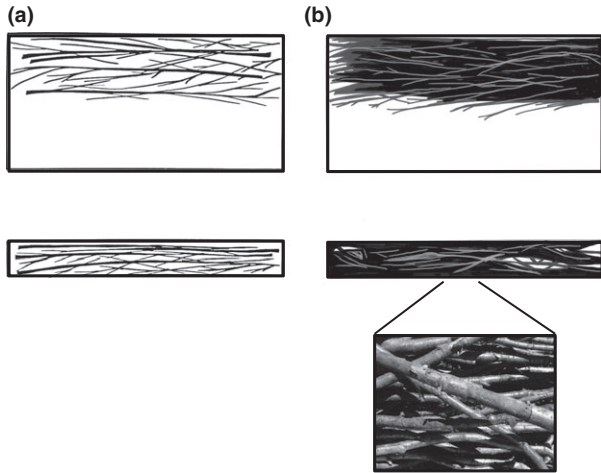


Fig. 1. (a) Schematic picture of the intermediate FW treatment, from above and from one side. (b) Schematic picture of the high FW treatment, from above, from one side and a zoomed-in photograph. The pictures from above show the FW accumulations covering half the bottom substrate, closest to the windowless wall of the aquarium. The pictures from one side show the FW accumulations in the background. The waterbody lacking FW is in front of the FW.

Fish acquisition and keeping

A total of 36 young-of-the-year (0+) trout (fork length 45–65 mm) were collected by electrofishing from the river Tvärån (latitude 59°N) on 21 and 24 August and on 9 October 2012. The trout were brought to the laboratory and placed in groups of 5–6 individuals in 200 litre tanks with circulating, filtered tap water at a temperature of 13 °C and a 12:12 h photoperiod. Each tank contained 6–8 shelters (halved clay pots) and was supplied with a front curtain. All fish were allowed to acclimate for at least 3 weeks. During this time, they were fed 10 thawed red chironomid larvae per tank three times a week. Fish that were reluctant to start eating were also fed 5–6 live Ephemeroptera, Diptera and Trichoptera larvae on two to three occasions during this period. After 3 weeks, the fish were kept separately in 200 litre tanks, each divided into three separate compartments with one fish in each. Food rations were increased to 0.25 g of chironomids per fish and week. On 15 and 16 November, fish were anaesthetised with benzocain and tagged with visible implant elastomer (VIE) alongside the anal fin (as described by for example Olsen & Vøllestad 2001). Thereafter, the fish were kept in groups of four in 200 litre tanks, with each individual fish in the group having its own VIE-tag colour (orange, red, green or blue).

Experimental design

Our design was set up to detect effects of FW density, number of fish in the channel and possible

interactions between those two variables. Trials were performed 22 November–29 December 2012. The nine groups of four fish were tested once in each FW treatment. Also, from the 36 fish individuals, 26 were chosen randomly to participate in single-fish trials. Eleven single-fish trials per FW treatment were performed. Each single-fish individual was observed in either one or two FW treatments. A schedule for the fish participating in the trials was made before the experiment started, so that the proportion of single- and four-fish trials each day was determined randomly, and the prerequisite was fulfilled that all fish rested at least 4 days between trials. Twenty hours before each trial, fish were transferred from the holding tanks to the stream channels. During each trial, observations of swimming, foraging, aggression and sheltering were recorded with a digital video camera from behind a curtain. Each trial began between 08.00 and 10.00 a.m., with 3 min of observation and video recording. Thereafter, 0.5- to 1-cm-long thawed red chironomid larvae were flushed into the stream channel through a tube that emerged *c.* 10 cm below the water surface. To avoid disturbing the trout, water was continuously flushed through the tube, and larvae were added through a funnel from behind a curtain. One larva was released every 15th second until a total of 10 larvae were released. Observation and video recording continued for another 2.5 min after feeding had ended. The procedure was repeated for the two other stream channels. All fish were then returned to their respective holding tank, and left-over chironomid larvae were removed from the stream channel. Video recordings of groups of four fish were ended by a quick zoom-in on the visible individuals, so the VIE-tag could be seen. When analysing the video recordings, they were back-tracked to ensure that the four individuals were correctly recognised throughout the observation period.

Protocol and statistical analysis

Video recordings were used to determine the amount of time the trout spent (i) for all movements >0.5 fish body lengths; (ii) cruising, defined as movement at speeds from 0.5 to 2 body lengths per second; (iii) holding focal point; (iv) successfully attacking drifting prey, defined as the movement from the focal point to the point where the prey was caught and back; (v) unsuccessfully attacking drifting prey; (vi) attacking prey on the bottom substrate; (vii) making aggressive attacks; and (viii) hiding in the FW. Fish not visible at all during the trial were included in the analyses and assumed to be passive, not foraging, not engaged in aggressive encounters, and, for the two FW treatments, hidden in FW. Behaviour during feeding (2.5 min) and after feeding (2.5 min) was

quantified. The proportion of time allocated to the various behaviours was calculated from these quantifications. Furthermore, we counted the number of prey taken, the number of aggressive attacks per minute averaged over the four individuals in the four-fish groups and also the number of aggressive attacks per minute and aggressive individual. For foraging data, only the time during feeding was analysed.

All data were analysed by two-way factorial ANOVA with FW density and number of fish in the channel as fixed factors, except data for aggression, which were analysed only for the four-fish groups by one-way factorial ANOVA with FW density as fixed factor. Proportional data were square-root-arcsine-transformed, and count data were $\log_{10}(x + 1)$ -transformed prior to statistical analysis. The single-fish trials were represented by data from the single fish per replicate, whereas the four-fish groups were represented by the mean value of the four fish per replicate. Exceptions to this were analyses of capture success and aggressive rate, where only data of foraging and aggressive fish were included.

Results

Total activity of the trout (i.e. all activity due to swimming, foraging, aggression and other movements) declined in both single-fish trials and four-fish trials from 28% at the no FW density to 20% at the intermediate FW density and 17% at the high FW density. However, neither FW density nor number of fish in the channel had any significant effect on the proportion of total activity (two-way ANOVA, $F_{2,54} = 1.198$, $P = 0.310$ for FW density, $F_{1,54} = 0.903$, $P = 0.346$ for number of fish in the channel, $F_{2,54} = 0.018$, $P = 0.982$ for the interaction; Fig. 2). Most of the time was spent passive (Fig. 2), and also, in 70% of the single-fish trials, the fish was completely passive throughout the trial. Of the individuals in the four-fish group trials, 44% were completely passive throughout at least one trial. Passive fish spent their time either sheltering in the FW or resting at the bottom gravel without overhead cover. More time was allocated to holding focal point than to other activities (Fig. 2).

Cruising

Two-way ANOVA revealed a significant effect on time spent cruising of FW density ($F_{2,54} = 3.796$, $P = 0.029$) and of number of fish in the channel ($F_{1,54} = 4.558$, $P = 0.037$) but no interaction ($F_{2,54} = 1.539$, $P = 0.224$). The trout spent 2.4% of their time cruising at the no FW density, 0.8% at the intermediate and 0.5% at the high FW density (Fig. 3). Averaged over all groups, 1.2% of the time was spent cruising. Furthermore, fish spent less time

cruising when alone than in the four-fish groups (0.9% vs. 1.5%; Fig. 3).

Time spent in the FW

A two-way ANOVA revealed a significant effect of FW density on time spent sheltering ($F_{1,36} = 4.189$, $P = 0.048$) but no effect of the number of fish in the channel ($F_{1,36} = 0.429$, $P = 0.510$) or the interaction ($F_{1,36} = 0.854$, $P = 0.361$; Fig. 4). In the two treatments with FW, the trout spent on average 71% of the time in the FW. At the intermediate and high FW densities, the percentages were 59% and 83% respectively. Fifty-six per cent of the fish individuals at the intermediate FW density hid in the FW during the entire trial, and 81% of the individuals did so at the high FW density. Only 13% of the fish at the intermediate FW density and 10% of those at the high FW density changed between habitats with and without FW. Video analyses also showed that trout were more often found <5 cm above the bottom substrate than elsewhere in the water column in all three FW treatments.

Foraging

We found a significant effect of FW density on the proportion of time spent for successful prey attacks, but no effect of the number of fish in the channel, and no interaction (two-way ANOVA, $F_{2,54} = 3.594$, $P = 0.034$ for FW density, $F_{1,54} = 1.315$, $P = 0.256$ for number of fish in the channel, $F_{2,54} = 0.084$, $P = 0.919$ for the interaction effect; Fig. 5). Scheffé's *post hoc* test confirmed a difference between no FW and intermediate FW density ($P = 0.040$). The trout spent on average 1.5% of their time on successful attacks on drifting prey. This proportion was 0.7% at the intermediate FW density and 2.5% at the no FW density. At the high FW density, it was 1.3%.

FW density had a significant effect on capture success, measured as the proportion of attacked prey items that were caught and eaten by foraging fish, but we found no effect of the number of fish in the channel, and no interaction (two-way ANOVA, $F_{2,23} = 3.652$, $P = 0.042$ for FW density, $F_{1,23} = 0.751$, $P = 0.395$ for number of fish in the channel, $F_{2,23} = 0.187$, $P = 0.831$ for the interaction effect; Fig. 6). Capture success was highest at the no FW density, with c. 90% of attacked prey caught. At the intermediate and high FW density, 50–67% and 82–92% were caught respectively (Fig. 6). Scheffé's *post hoc* test confirmed a difference between the success at the no FW and intermediate FW density. However, capture success did not differ significantly between the no and high FW density, neither between the intermediate and high FW density.

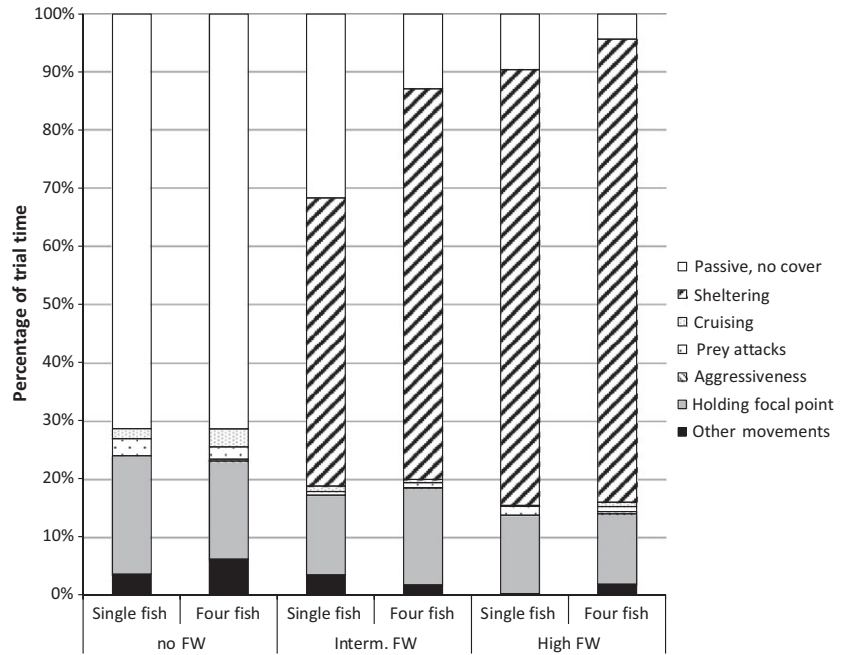


Fig. 2. Mean percentage of total trial time spent for different behaviours.

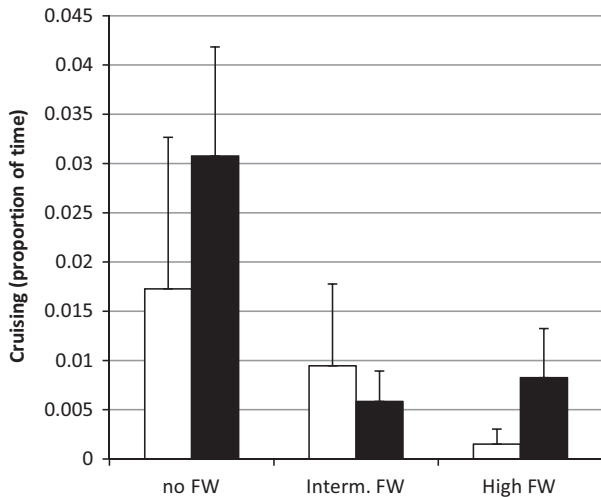


Fig. 3. Proportion of time spent cruising (mean + SE) by fish when alone and in the four-fish groups at the three FW densities. Filled bars represent trout in four-fish groups ($N = 9$), and open bars represent single trout ($N = 11$).

We found no significant effects of FW density or number of fish in the channel on other measures of foraging, such as the proportion of time spent for failed attacks on drifting prey (two-way ANOVA, $F_{2,54} = 0.532$, $P = 0.590$ for FW density, $F_{1,54} = 2.268$, $P = 0.138$ for number of fish in the channel, $F_{2,54} = 0.759$, $P = 0.473$ for the interaction effect), the time spent holding focal point (two-way ANOVA, $F_{2,54} = 2.079$, $P = 0.135$ for FW density, $F_{1,54} = 1.335$, $P = 0.253$ for number of fish in the channel, $F_{2,54} = 0.074$, $P = 0.929$ for the interaction effect), the time spent for attacks on prey that had fallen onto the bottom gravel (two-way ANOVA,

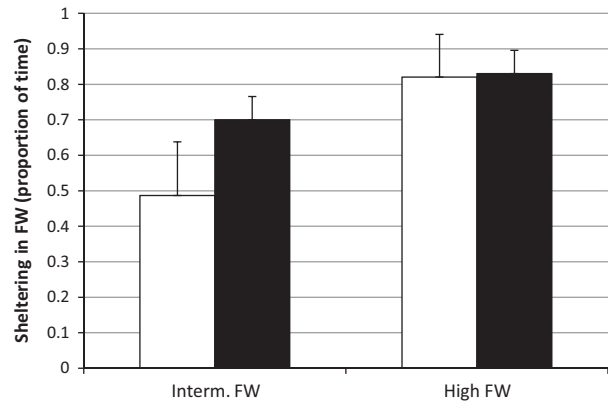


Fig. 4. Proportion of time spent in FW (mean + SE.) by fish when alone and in groups of four at the two FW densities. Filled bars represent trout in four-fish groups ($N = 9$), and open bars represent single trout ($N = 11$).

$F_{2,54} = 0.627$, $P = 0.538$ for FW density, $F_{1,54} = 0.014$, $P = 0.907$ for number of fish in the channel, $F_{2,54} = 1.409$, $P = 0.253$ for the interaction effect) or the rate of feeding, measured as the average number of prey taken per minute (two-way ANOVA, $F_{2,54} = 1.301$, $P = 0.281$ for FW density, $F_{1,54} = 0.193$, $P = 0.662$ for number of fish in the channel, $F_{2,54} = 0.171$, $P = 0.843$ for the interaction effect).

Aggression

Several measures of aggression were analysed – average number of aggressive attacks per individual and minute, number of aggressive attacks per aggressive individual and minute and average pro-

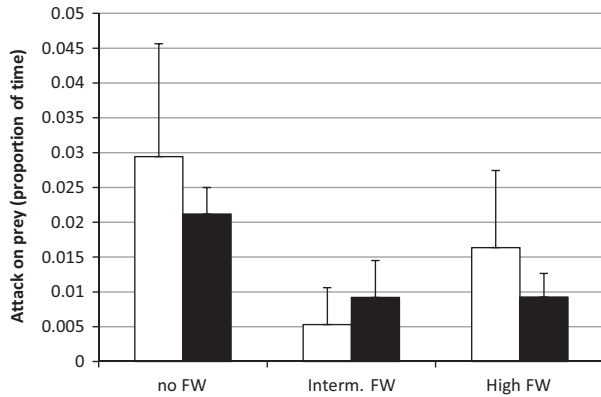


Fig. 5. Proportion of time spent for successful attacks on drifting prey (mean + SE) by fish when alone and in groups of four at the three FW densities. Filled bars represent trout in four-fish groups ($N = 9$), and open bars represent single trout ($N = 11$).

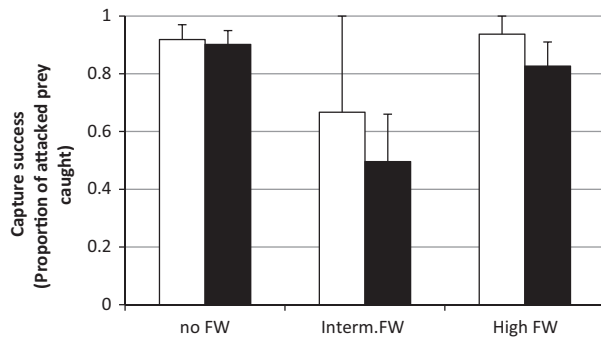


Fig. 6. Capture success of foraging fish (proportion of attacked prey caught, mean + SE). Open bars are for single-fish individuals ($N = 4$ at no FW, $N = 3$ at intermediate FW, $N = 2$ at high FW density), and filled bars for mean success of foraging individuals in four-fish groups ($N = 9$ at no FW, $N = 6$ at intermediate FW, $N = 5$ at high FW density).

portion of time spent for aggressive attacks. However, we found no significant effects of FW density (one-way ANOVA $F_{2,24} = 1.272$, $P = 0.298$ for average number of aggressive attacks per individual and minute, $F_{2,6} = 0.325$, $P = 0.734$ for number of aggressive attacks per aggressive individual and minute and $F_{2,23} = 0.874$, $P = 0.431$ for proportion of time spent for aggressive interactions). Only six individuals were aggressive at all – three of them showed aggression at the no FW density, one at the intermediate FW density and four at the high FW density. The number of aggressive acts per minute and aggressive individual was 0.1–0.5, 0.1 and 0.1–0.7 at the no, intermediate and high FW densities, with a trend towards higher average aggression at the no FW density (Fig. 7).

Discussion

In the present study, we examined effects of three FW densities on 0 + brown trout, alone and together

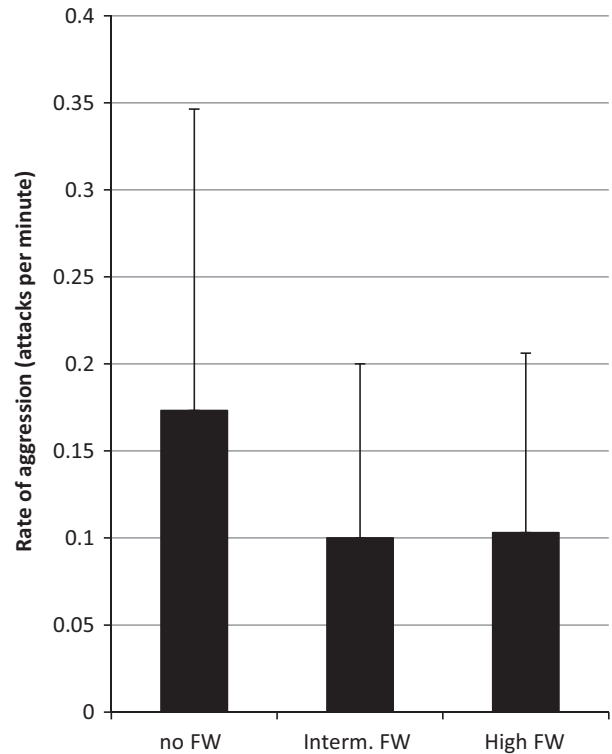


Fig. 7. Number of aggressive attacks per minute and aggressive individual (mean + SE; $N = 3$ in no FW, $N = 1$ in intermediate FW, $N = 4$ in high FW density) at the three FW densities in the four-fish group.

with conspecifics, under controlled conditions in artificial streams. The stream channels mimicked stream conditions with no, intermediate and very high densities of FW. By bringing in stream-conditioned FW and 0 + trout from a wild population, we created conditions in terms of FW and fish density found in small local forest streams. Also, we chose temperature, bottom substrate and water velocities that are typically found in the native stream of the trout used in the experiment. Therefore, our results should reflect the behaviour of trout in natural stream habitats.

The first of our hypotheses, that we would find a decrease in activity with increasing FW density, was supported. The finding that FW decreases trout cruising time is consistent with other studies, showing that fish activity rates are dependent on access to shelters (Kalleberg 1958; Harvey et al. 1999; Sundbaum & Näslund 1998; Gustafsson et al. 2012; but see Kemp et al. 2005). Our study showed a 67% decrease in cruising time when FW was introduced, which is similar to the 74% decrease in activity reported by Gustafsson et al. (2012) for single small trout in habitats with added large wood (LW). Also, total average trout activity in our study (21.7% of time) was similar to the 27.7% activity of small trout in the study with LW. However, the single small fish of our

study were more active in the intermediate and high FW environments than those observed at the corresponding LW densities (Gustafsson et al. 2012).

In-stream structure is known to attract stream salmonids (Culp et al. 1996; Roni & Quinn 2001), but the character of the structure seems to be crucial in determining the response of the fish (Culp et al. 1996; Whiteway et al. 2010; Langford et al. 2012). FW and LW represent different types of habitat complexity, and the local abundance of small salmonids is increased by FW but not by LW (Culp et al. 1996; Antón et al. 2011; Langford et al. 2012). Also, large in-stream structures cause increases in density and biomass of large rather than small salmonids (Whiteway et al. 2010). Our study shed light on sheltering and position choice of small trout in FW, which may differ from small trout behaviour in LW environments. In our study, trout spent on average 71% of their time close to the bottom in the FW when they had access to it, which suggests that the FW may have been an attractive shelter for the trout. The FW covered bottom areas of equal size at the intermediate and high FW densities, but in spite of this, the time spent in the FW was higher at the high FW density, presumably because it provided more visual isolation and therefore was a shelter of higher quality. This is different from the results of LW studies, where small trout chose positions on top of or beside the logs (Gustafsson et al. 2012).

The proportion of time spent cruising in our study was higher in the four-fish groups than when fish were alone. This is consistent with earlier studies, showing more activity when fish density is higher, often as a result of more agonistic interactions between individuals (Cole & Noakes 1980; Cooke et al. 2000; Gustafsson et al. 2012; but see Fender-son & Carpenter 1971). In our study, cruising seemed not to be caused by agonistic interactions or by a need to disperse to maintain separation from other fish in the four-fish groups. The actual cause of cruising was not possible to determine, and therefore, all swimming in a certain speed interval was included in the cruising category. The total activity level, however, did not differ between the four-fish groups and the single fish of our study. Indeed, the presence or absence of conspecifics did not affect any of our outcome measures except the cruising time, which is surprising as there is ample evidence of density dependence in stream-living fish (Jenkins et al. 1999; Grant & Imre 2005; Imre et al. 2005; Lobón-Cervía 2007; Vøllestad & Moland Olsen 2008). The lack of density-dependent effects on measures other than cruising time might have been caused either by too low fish density to give overall effects on fish behaviour (c. 2.3 fish per m² in the four-fish groups) or by the familiarity of the fish. The fish included in our

study were kept together in the holding tanks, and familiar fish focus less attention on aggression than unfamiliar fish do (Griffiths et al. 2004), which is supposed to lead to a lower activity level.

Differences in habitat complexity and habitat preference can affect territory defence behaviour (Basquill & Grant 1998; Johnsson et al. 2000; Gustafsson et al. 2012). However, our prediction of decreased aggression with increased FW density was not supported. This was probably due to that we used average values of aggression in our statistical analyses, which moderated the large difference in aggression between different-ranked fish. The general level of aggression found in our study corresponds with earlier research on 0+ brown trout, reporting rates of individual aggressive behaviour ranging from 0.15 to 0.6 aggressive acts per minute and aggressive individual (Griffiths et al. 2004), to be compared with the 0.1–0.7 aggressive acts per minute found in our study. However, few fish individuals were aggressive at all in our study, maybe because they were familiar and thus less likely to be involved in agonistic behaviour towards each other (Griffiths et al. 2004). To further elucidate the effect of FW on trout behaviour, experiments should be designed to compare behavioural responses according to individual social status.

The hypothesis that foraging would decrease with increasing FW density was supported, as we found both a lower capture efficiency and lower proportion of time allocated to foraging at the intermediate than at the no FW density. This is consistent with other studies, suggesting that habitat structure may impede localisation of and attack on prey both in brown trout and other fish species (Savino & Stein 1982; Wilzbach et al. 1986; Sundbaum & Näslund 1998) and that in-stream structure can decrease foraging in drift-feeding fish (O'Brien & Showalter 1993; Gustafsson et al. 2012). Interestingly, capture success at the high FW density did not differ from the success in either of the two other treatments. This may be due to a behavioural change when FW density increased; only a few individuals foraged at the high FW density while all others sheltered, as compared to the intermediate FW density, where fewer trout sheltered and more foraged. This meant a higher average capture success in high FW trials, where the few foraging individuals were able to hunt undisturbed and catch almost all prey offered, whereas in intermediate FW trials more than one individual could try to catch the same prey. The small number of foraging fish at high FW densities could be interpreted as a density-dependent effect, that is the foraging fish may have monopolised the food resources, forcing subordinate fish to shelter. It is, however, challenging to determine whether this was the case, or if the fish in the FW

sheltered voluntarily. Interestingly, however, two of the seven foraging individuals at high FW density repeatedly moved out of the FW to catch prey and then entered the FW again to shelter. This behaviour suggests that at least these individuals could choose to forage or shelter at any given moment. However, this choice existed only for fish sheltering relatively close to the open water. Fish sheltering far from the open water presumably experienced a low encounter rate of prey due to the FW, as it was difficult or impossible to reach drifting prey in time when twigs and branches interfered with fish movement. However, predators can change their foraging mode in response to structural complexity (James 1994; Michel & Adams 2009), and it is possible that trout in natural streams feed epibenthically while sheltering, thus changing their sit-and-wait foraging strategy to active search for prey. Some of the fish individuals in our study were observed swimming around slowly and nibbling the surface of the wood, as if searching for epibenthic prey.

Sheltering in salmonids is known to be density dependent. Available shelters will soon be occupied and defended, and no more individuals will get access to the shelters (Armstrong & Griffiths 2001). We hypothesised that trout would spend more time in FW in four-fish groups than when alone, as we assumed that the four-fish density would be low enough for giving all fish access to shelter, and also, that fish would seek shelter to avoid interactions with aggressive conspecifics. However, we found no support for this hypothesis. Instead, we found a nonpredicted increase in time spent in FW when FW density increased. We propose that this is because FW was a more attractive habitat when it was denser, possibly conveying benefits to the fish in a way similar to habitats with many separate sheltering structures (Finstad et al. 2007). Other potential explanations such as avoidance of high water velocity or aggressive conspecifics are less likely, as water velocity was zero close to the bottom outside of the FW, where passive trout outside of the FW resided. In addition, aggression levels were low and sheltering behaviour common also when fish were alone. One could speculate that sheltering was a predator avoidance behaviour rather than avoidance of current or conspecifics. However, causes for sheltering must be further explored by other studies focusing specifically on this question.

Our findings have relevance to the management of brown trout streams. If recruitment of trout fails in spite of good spawning areas, addition of FW to the stream may be considered to improve the habitat of young-of-the-year trout and thereby increase the carrying capacity of the stream. This should provide the greatest benefits in streams with high current

velocities and lack of other suitable shelters for small fish (Armstrong & Nislow 2006) and in streams where trout survival is decreased by predators, for example mink (Heggenes & Borgström 1988). Also, the role of FW in stream ecosystems should be considered in forest management, for example by restrictions on forest harvesting in stream riparian zones.

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