

Shelter availability affects behaviour, size-dependent and mean growth of juvenile Atlantic salmon

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SUMMARY

1. Anthropogenic disturbances of the physical habitat and corresponding effects on fish performance are key issues in stream conservation and restoration. Reduced habitat complexity because of increased sediment loadings and canalization is of particular importance, but it is not clear to what extent fish populations are influenced directly by changes in the physical environment, or indirectly through changes in the biotic environment affecting the food availability.

2. Here, we test for the direct effect of habitat complexity on the performance (growth) of juvenile Atlantic salmon by manipulating shelter availability (interstitial spaces in the substrate) across 20 semi-natural stream channels without altering the substrate composition, and stocking each channel with a common density of fish. A simple method for measuring salmonid shelters using flexible PVC tubes was developed and tested. Daytime sheltering behaviour and growth rates were compared across the channels differing in shelter availability.

3. Measured shelter availability was strongly negatively correlated with observed number of fish not finding shelters and mass loss rates of the fish (growth performance) increased with decreasing number of measured shelters. Number and mean depth of interstitial spaces explained up to 68% and 24% of the among-channel variation in sheltering behaviour and growth performance, respectively. Furthermore, negative effects of shelter reduction increased with fish body size. Thus, changes in habitat structure may even influence the size selection gradients.

4. Shelter availability is an easily measured variable, possibly affecting the population demographics and long-term evolutionary processes, and is therefore a key habitat factor to be considered in stream restoration and habitat classification.

Key words: competition, growth, habitat restoration, *Salmo salar*, substrate embeddedness

Introduction

Anthropogenic disturbance of the physical habitat is a key issue in stream conservation and restoration. Alterations of the physical stream habitat associated with canalization or increased sediment load because of hydropower development, road building, deforestation and agriculture may impact population demo-

graphic rates and ultimately broader patterns of biodiversity (Miller, Williams & Williams, 1989; Waters, 1995; Giller, 2005; Lepori, Palm & Malmquist, 2005). There is a growing body of evidence that decreased habitat complexity and increased substrate embeddedness negatively impacts the survival and growth of freshwater organisms (Crouse *et al.*, 1981; Miller *et al.*, 1989; Nehlsen, Williams & Lichatowich, 1991; Frissell, 1993; Suttle *et al.*, 2004). Candidate mechanisms are reduced shelter availability which may increase predation risk, causing reduced survival (Babbitt & Tanner, 1998; Forester & Steele, 2004;

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Arthur, Pech & Dickman, 2005) or altered behaviour reducing physiological performance (Arthur, Pech & Dickman, 2004; Millidine, Armstrong & Metcalfe, 2006), and changes in prey availability caused by the habitat changes (Waters, 1995; Negishi, Inoue & Nunokawa, 2002; Suttle *et al.*, 2004).

Anadromous salmonid fishes are among those fish species commonly found in landscapes with a high degree of anthropogenic impact. Many salmonids spend from one to several years after birth in streams before migrating to sea, and density-dependent processes are prevalent during the freshwater stage, suggesting strong competition for suitable habitats (Elliott, 1994; Jonsson, Jonsson & Hansen, 1998; Einum, 2005; Dolinsek, Grant & Biron, 2007). Thus, degradation of stream habitats from external stressors such as land-use changes in the catchment areas or internal disturbances such as engineering of river channels may be one of the contributing factors to the negative trend in these populations (e.g. Parrish *et al.*, 1998).

So far, field and laboratory studies (e.g. Smith & Griffith, 1994; Suttle *et al.*, 2004) have compared salmonid performance in very different substrate qualities (e.g. fine sand versus coarse gravel) which may differ both in shelter and food availability, making it difficult to separate the effects of the two factors. A functional understanding of the role of habitat complexity for the performance of juvenile salmonids is therefore still lacking despite considerable scientific and political motivation to evaluate the effects of habitat degradation and compensation efforts. Furthermore, anthropogenic habitat disturbance may induce changes in adaptive landscapes affecting contemporary evolution (Stockwell, Hendry & Kinnison, 2003; Hendry *et al.*, 2006), but it is not known to what extent changes in substrate structure influences the relative performance of different salmon phenotypes.

Here, we test how shelter availability *per se* changes the performance and size selection gradients of juvenile Atlantic salmon (*Salmo salar* L.). We manipulated the embeddedness in semi-natural stream channels without altering the particle size composition of the substrate. Currently, methods for quantifying substrate quality and embeddedness are based on the various measures of particle sizes or substrate morphology scales (Waters, 1995; Sylte & Fischenich, 2002). Although these may correlate with shelter

abundance, they do not offer a direct measurement of interstitial spaces available as shelters for the fish. We therefore also developed new method for quantifying the number and size of shelters, and tested the method by comparing the number of non-sheltering fish in stream channels stocked with a common density of juvenile Atlantic salmon with measured shelter availability. The experiment was carried out during winter, a period when shelters are considered to be of particular importance to juvenile salmonids (Smith & Griffith, 1994; Valdimarsson & Metcalfe, 1998).

Methods

The experiment was conducted at the NINA Research Station, Ims (southwestern Norway, 58° 54'N, 5° 57'E). The fish used in the experiments were one summer old (0+) first generation hatchery reared Atlantic salmon with parents originating from the River Lone (60° 11'N, 5° 30'E). Hatchery-reared Atlantic salmon have been shown to use shelters in a similar way to wild salmon, but they tend to share shelters more often than their wild conspecifics (Griffiths & Armstrong, 2002). Thus, the use of hatchery fish makes the present experiment conservative with regard to detecting effects of shelter availability on performance.

The experimental set-up consisted of 20 semi-natural stream channels (485 × 25 cm, water depth *c.* 30 cm) with a water flow of 34.4 (± 3.9 SD) l min⁻¹. Water to the hatchery and the channels is drawn from a nearby lake. Water temperatures ranged from 2.3 to 1.4 °C during the experiment, which is well below temperatures where juvenile Atlantic salmon attain a winter behavioural pattern and sheltering during daytime (*c.* 10 °C; Fraser, Metcalfe & Thorpe, 1993; Heggenes *et al.*, 1993). No food was added during the experiment, and thus only natural food items entering through the inlet water, or present in the substrate, were available for the fish. Because of similar inlet water-source and identical substrate composition among channels, invertebrate drift rates should be low and similar across the channels. Monofilament lines were stretched across each stream channel to reduce the risk of predation from birds. Equal size distribution of natural substrate across channels was achieved by first adding a *c.* 5-cm layer of gravel (mean diameter 4.3 cm ± 1.8 SD) and subsequently

evenly distributing eight larger rocks (mean diameter $19.4 \text{ cm} \pm 4.2 \text{ SD}$) in each channel. To obtain a gradient of shelter availability among the channels, while keeping substrate size composition constant, variable numbers of the rocks were embedded approximately 2 cm in the gravel substrate. The number of embedded rocks in each stream channel varied from zero to eight and each treatment was duplicated except for treatments with zero and eight embedded rocks, which were triplicated. The distribution of treatments (number of embedded rocks) among stream channels, as well as the within channel position of the embedded rocks, was assigned at random to avoid systematic channel effects and effects of embedded rock position relative to the water inlet. As the submergence of embedded rocks into the substrate was minor and the water velocities were generally low ($<0.5 \text{ cm s}^{-1}$), the environmental conditions are likely to be similar across the channels and treatments, besides the intended differences in shelter availability.

For each channel, shelter abundance was quantified by first identifying potential interstitial spaces visually. For each such space, we measured its depth with flexible PVC tubes (commercial available as e.g. aquaria accessories) of five different diameters (5, 10, 13, 16, 22 mm) (Fig. 1). For each tube diameter, only spaces deeper than 3 cm (25–38% of body length of the fish) were counted as a shelter. Thus, for each channel, we obtained five different measures of total shelter numbers and mean shelter depths, one for each tube diameter. Each single entrance to an interstitial space was defined as a shelter (i.e. an Y-shaped cavity under a single rock would be counted as three shelters).

Ten juvenile Atlantic salmon were released in each stream channel 26 January 2006 after being individually tagged (PIT), measured ($\pm 1 \text{ mm}$), and weighed ($\pm 0.01 \text{ g}$). Wet mass ranged from 4.64 to 18.07 g (mean $10.92 \pm 3.17 \text{ SD}$), total length from 80 to 121 mm (mean $105 \pm 9 \text{ SD}$) and body depth (measured at the anterior base of the dorsal fin) from 14 to 22 mm (mean $19 \pm 2 \text{ SD}$). There was no difference in initial mass or length of the fish among channels (all $F_{19,199} = 0.41$, all $P = 0.989$). Prior to termination of the experiment (on 20 and 21 February), we observed the number of fish not obtaining shelters by observing the stream channels from a few metres distance using binoculars. To ensure that fish in close vicinity to

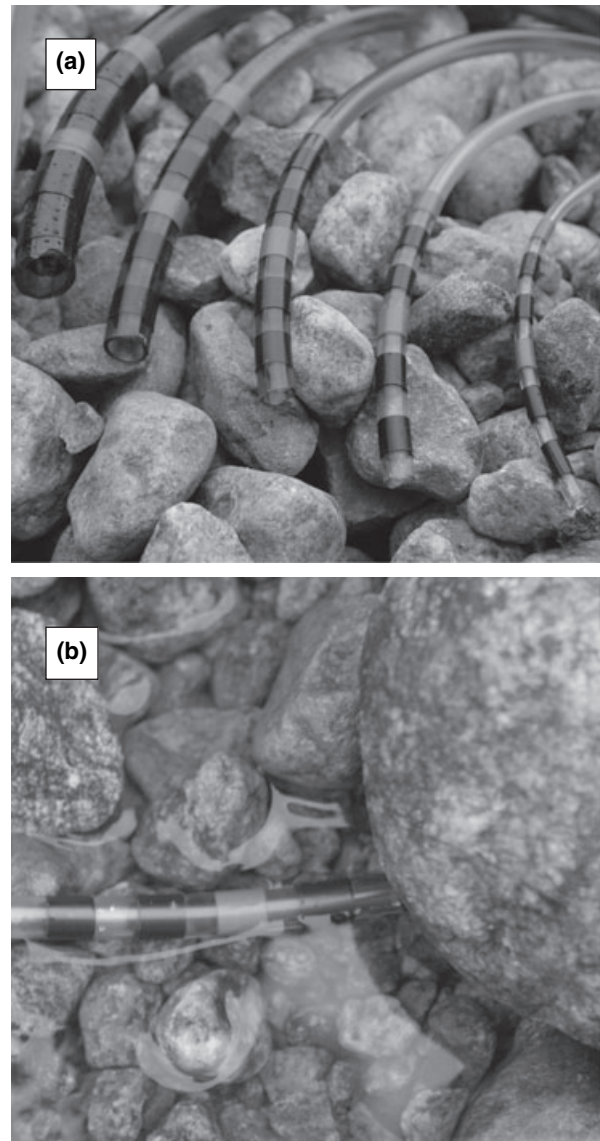


Fig. 1 (a) PVC tubes of five different diameters (from left to right; 22, 16, 13, 10 and 5 mm) used for quantifying interstitial spaces in the substrate. (b) Measurement of interstitial space under non-embedded rock.

rocks that did not shelter were observed, two persons were simultaneously observing from behind a blind screen at each end of the channel. The observers recorded the position of each observed fish on a map, and recordings were subsequently cross-checked to obtain the number of visible fish. Observed fish were either registered as non-sheltering (the whole fish visible) or partially sheltering (parts of the fish visible; typically tail not covered by the shelter). Each channel was observed at dawn, mid-day and before dusk

during each of two consecutive days, and the averages of all observations were used in the subsequent analyses. The mean numbers of non-sheltering and partially sheltering fish in each stream channel were compared to shelter availability (number and mean depth of shelters measured with each tube diameter) using a set of multiple regressions.

No mortality occurred during the experiment and at the end of the experiment (22 February), the channels were drained and all fish retrieved. The fish were killed by an overdose of anaesthetics, weighed, and the occurrence of stomach content registered. Performance was measured as daily specific growth rate:

$$(\ln M_{\text{end}} - \ln M_{\text{start}})/t \quad (1)$$

Where M_{end} is wet mass at end, M_{start} is wet mass at start of the experiment and t is the duration of the experiment in days.

As a measure of size selection gradients within each stream channel, we obtained the slope coefficient for the linear regression of individual wet mass at the start of experiment against wet mass at the end of the experiment (all $P < 0.001$, all $R^2 > 0.92$). The relationship between start and end mass was linear within the current experimental period and no residual deviation from normality or inflation of variance was detected. A systematic variation in the steepness of the regression between different treatments would indicate that there are effects of the treatment on the relative performance of different size classes. For example, a higher slope coefficient would indicate that smaller fish performed relatively better than large. To test for the effects of shelter on size-related performance, we therefore regressed the slope coefficients against the number of measured shelters. To remove the effect of among channel differences in mean performance (growth rate) on slope coefficients, growth rate was also included in the analyses, resulting in a multiple regression model testing for the effect of growth rate and shelter availability on the regression coefficients.

Results

The number of shelters varied greatly among channels, and there were strong negative correlations between the number of embedded rocks and the number and size of measured shelters in each stream channel (Table 1). Thus, the manipulation of embedd-

Table 1 Correlations coefficients (R) and significance levels (P) for the correlations between number of embedded rocks in the stream channels and measured number and depths of shelters ($n = 20$) as well as range of measurements

Tube (mm)	Number of shelters			Mean depth of shelters		
	R	P	Range	R	P	Range
5	-0.80	<0.001	3–19	-0.60	0.006	4–9
10	-0.89	<0.001	0–17	-0.56	0.011	0–9
13	-0.90	<0.001	0–14	-0.36	0.121	0–9
16	-0.75	<0.001	0–11	-0.65	0.002	0–7
22	-0.45	0.044	0–6	-0.36	0.114	0–7

edness was successful in creating a range of shelter availabilities among channels.

Mean number of fish observed in each stream channel ranged from 2.3 to 9.9. The number of non-sheltering fish (the complete body visible) varied accordingly (range: 0.2–8.3), and was highly correlated with the total number of observed fish (including partially sheltering) (Pearson's $R = 0.88$, $P < 0.001$, $n = 20$). The mean number of whole fish observed decreased with increasing number of interstitial spaces measured with the three smallest tube diameters (Table 2). Total number of observed fish (including partially sheltering) decreased with both increasing

Table 2 Multiple regressions testing for effects of number and mean depths of shelters on the number of observed juvenile Atlantic salmon (ln transformed) across 20 stream channels. Models are fitted on both (a) number of whole fish observed (i.e. non-sheltering) and (b) total number of observed fish (including both non- and partially-sheltering fish). Separate models are provided for measurements using different tube diameters. Unstandardized coefficients (β) for the effect of number and mean depths of shelters are also given

Tube (mm)	Number of shelters			Mean depth of shelters			R^2
	β	$F_{1,17}$	P	β	$F_{1,17}$	P	
(a)							
5	-0.142	9.14	0.008	-0.198	1.27	0.276	0.35
10	-0.141	8.49	0.010	-0.057	0.22	0.646	0.36
13	-0.157	9.17	0.008	-0.072	0.39	0.543	0.34
16	-0.144	2.17	0.159	-0.144	0.54	0.473	0.18
22	-0.004	0.00	0.986	-0.122	0.99	0.335	0.00
(b)							
5	-0.033	6.79	0.018	-0.198	17.74	0.001	0.60
10	-0.035	7.35	0.015	-0.100	9.54	0.007	0.61
13	-0.055	20.68	<0.001	-0.086	9.86	0.006	0.68
16	-0.057	5.07	0.038	-0.078	4.35	0.052	0.52
22	-0.087	1.88	0.188	-0.034	0.84	0.372	0.17

number and mean depth of interstitial spaces measured with all but the largest tube diameter (Table 2). Number and depth of spaces measured with the 13-mm tube best explained (highest R^2) the variation in fish sheltering between channels (Table 2, Fig. 2). The largest proportion of this variation was explained by number of interstitial spaces (numbers only, $R^2 = 0.53$; full model, $R^2 = 0.68$).

All fish lost mass during the experiment (mean $0.7 \text{ g} \pm 0.4 \text{ SD}$), and mean daily specific growth rates ranged from -0.0032 to -0.0017 among stream channels. Mass loss decreased with increasing numbers of measured shelters (Table 3; Fig. 3), and the relationship was strongest for shelter availability measured with the 13-mm tube. There were also significant or marginally significant (P range from 0.018 to 0.077) negative relationships between growth rates and measured number of shelters for all but the largest tube diameters (Table 3). There were no significant effects of measured mean shelter depths on growth

for any of the tube diameters. Only 4% of the fish had remains of food in their stomachs and there was no detectable difference in the frequency of fish with stomach content among stream channels.

Size-dependent performance was measured as the slope coefficients for the regression between initial and final wet mass within each stream channel. The slope coefficients ranged from 0.88 to 1.00 (mean $0.95 \pm 0.03 \text{ SD}$) among channels and correlated both with mean growth and shelter availability (Multiple regression; growth, $F_{1,17} = 4.75$, $P = 0.055$; shelter, $F_{1,17}$, $P < 0.001$; $R^2 = 0.49$). Thus, size-dependent performance tended to scale negatively with mean growth rate in the channels (Fig. 4a), indicating that larger fish performed relatively better when overall mass loss was high. Furthermore, there was a highly significant negative relationship between shelter availability and the size-scaling coefficients after correcting for overall variation in growth. This relationship can be illustrated by plotting the residuals

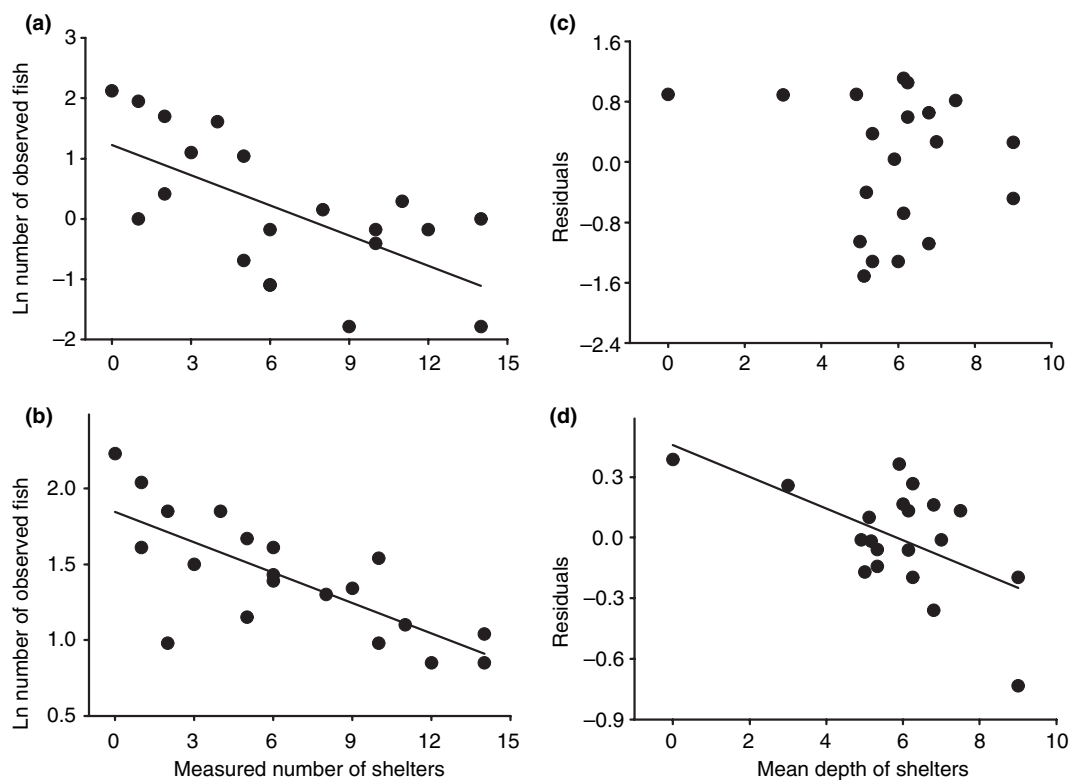


Fig. 2 Effects of measured number and mean depths of shelters on the number of observed juvenile Atlantic salmon across 20 stream channels. Relationships between measured number of shelters (using the 13-mm tube) and Ln number of (a) whole fish and (b) total number of fish observed (including partially visible fish), and residuals from these regressions plotted against the mean depth of shelters (c [residuals for a] and d [residuals for b]). Least square regression lines (a) $1.22 (\pm 0.37 \text{ SE}) - 0.67 \text{ shelters} (\pm 0.05 \text{ SE})$ ($R^2 = 0.40$), (b) $1.84 (\pm 0.11 \text{ SE}) - 0.07 \text{ shelters} (\pm 0.11 \text{ SE})$ ($R^2 = 0.55$), (d) $0.46 (\pm 0.11 \text{ SE}) - 0.08 \text{ shelter depth} (\pm 0.03 \text{ SE})$ ($R^2 = 0.30$).

Table 3 Multiple regressions testing for effects of number and mean depths of shelters on mean growth rates of juvenile Atlantic salmon across 20 stream channels. Separate models are provided for measurements using different tube diameters. Unstandardized coefficients (β) for the effect of number and mean depths of shelters are also given.

Tube (mm)	Number of shelters			Mean depth of shelters			R^2
	β	$F_{1,17}$	P	β	$F_{1,17}$	P	
5	3.5E-005	3.68	0.072	4.8E-005	0.48	0.496	0.13
10	3.9 E-005	4.44	0.050	4.8E-005	0.07	0.800	0.19
13	4.9 E-005	6.79	0.018	4.8E-005	0.05	0.823	0.24
16	6.1 E-005	3.55	0.077	4.8E-005	0.20	0.660	0.22
22	5.1 E-005	0.60	0.450	4.8E-005	1.30	0.271	0.10

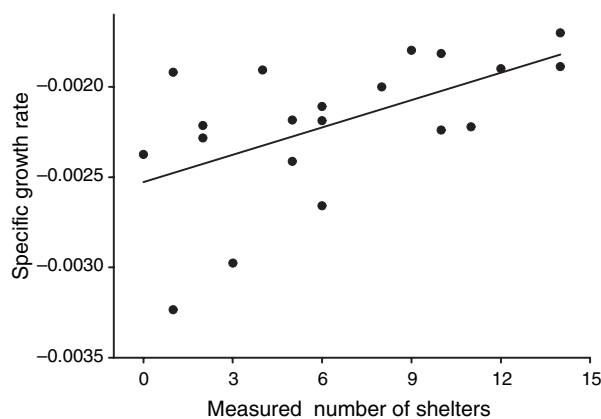


Fig. 3 Number of shelters measured (13-mm tube) in each stream channel against mean specific growth rate (performance) of the fish. Least square regression line; -0.003 (± 0.01 SE) + 0.00005 shelters (± 0.01 SE).

from the growth to coefficient relationship against shelter availability (Fig. 4b). Large fish were therefore more severely influenced by a reduction in shelter availability than smaller fish.

Discussion

By manipulating the shelter availability while keeping substrate size-composition constant, we demonstrate that increased availability of shelters significantly improves juvenile salmon performance. Our experimental design, and the lack of variation in stomach content across channels, makes it unlikely that substrate-induced differences in food availability or other environmental differences among treatments can explain the observed treatment effects. Improved performance in high-shelter environments was thus

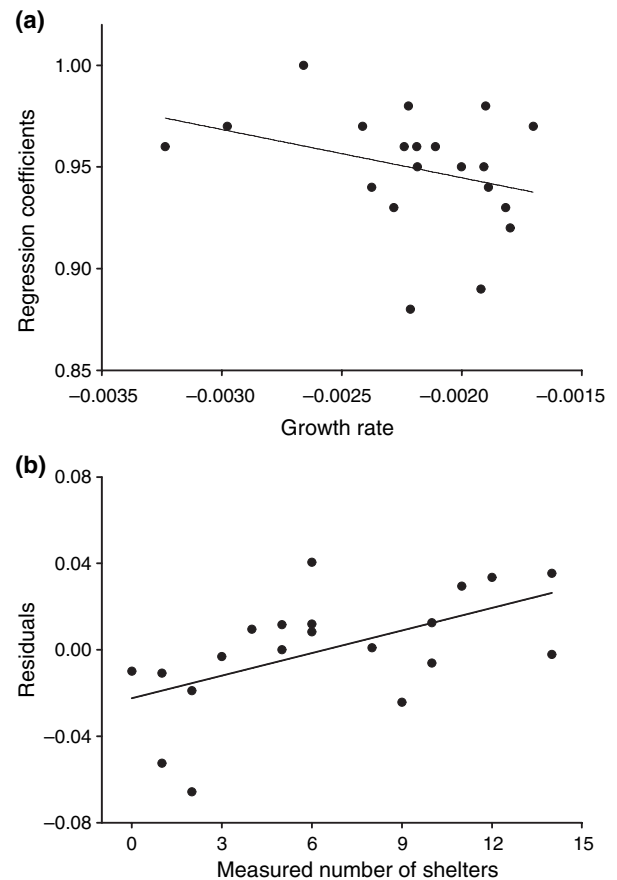


Fig. 4 (a) Regression slope coefficients from the relationship between wet mass at start and end of the experiment plotted against mean growth rate of the stream channels and (b) residuals from this relationship plotted against shelter availability, given as number of interstitial spaces measured using the 13-mm tube. Least square regression lines (a) 0.89 (± 0.03 SE) -23.74 Growth (± 16.67 SE) ($R^2 = 0.10$), (b) -0.022 (± 0.009 SE) + 0.004 shelters (± 0.001 SE) ($R^2 = 0.31$).

most likely caused by reduced metabolic costs. Juvenile salmonids in winter commonly have negative energy budgets, and the fish rely to a large degree on stored energy to survive. All fish in the present experiment had a net mass loss during the experiment of a magnitude comparable with that observed in wild Atlantic salmon during winter (Næsje *et al.*, 2006) and in previous experiments in semi-natural settings (Finstad *et al.*, 2004b). Individual survival probability is closely linked to the ability to retain storage energy above critical levels (Biro *et al.*, 2004; Finstad *et al.*, 2004a). Factors that negatively influence the energy budget during winter may therefore directly affect the population demography.

The physical structure of the habitat appears to be a key determinant of predation risk in most vertebrates (review by Lima, 1998), and habitat structure is an integrated part of predator-avoidance behaviour by reducing the detection probability of prey and providing the places to flee. Juvenile salmonids shelter in streambed interstices to avoid predators (Griffith & Smith, 1993; Heggenes *et al.*, 1993; Valdimarsson & Metcalfe, 1998), and the availability of shelters may therefore directly influence the mortality. The present study highlights that indirect effects of shelter availability may also influence the survival through impacts on individual energetic performance. A number of mechanisms may be responsible for such energetic effects. Anti-predator behaviour is commonly associated with reduced energy intake because of decreased foraging efficiency and increased predator alertness (Peckarsky *et al.*, 1993; Scrimgeour & Culp, 1994; VanBuskirk & Yurewicz, 1998). Thus, environments requiring higher levels of anti-predator behaviour may be less profitable energetically. For example, mammals have been shown to forage more actively in close proximity to structural complex habitats than in the open (Longland & Price, 1991; Abramsky *et al.*, 1996). Furthermore, house mice (*Mus musculus domesticus*) show lower growth and fecundity in low than in high complexity habitats (Arthur *et al.*, 2004). In the present experiment, the energy intake was probably very low as few fish appeared to have been feeding. The observed shelter effect was therefore most likely because of increased metabolic costs rather than the reduced energy intake. Lack of sheltering opportunities may increase maintenance metabolism in salmonids (Millidine *et al.*, 2006), probably because of the elevated levels of flight readiness (Hawkins, Armstrong & Magurran, 2004) or possible increased mental alertness. Salmonids are also known to compete for shelters during wintertime (Harwood *et al.*, 2002), and aggressive behaviour may have increased the energy expenditure. Finally, daytime resting in shelters may be energetically advantageous because of the reduced metabolism under the reduced light conditions (Finstad *et al.*, 2004b).

Reduction in the number of shelters also impaired the performance of larger individuals relative to smaller ones, likely because variation in shelter availability across treatments was more pronounced for the largest individuals. Small shelters (measured

with the smallest tube-diameters), which may be utilized by the smallest individuals, were available also in replicates with a high degree of embeddedness, whereas the largest shelters lacked almost completely. Because juvenile growth rate is strategic and may be optimized (Conover & Schultz, 1995; Arendt, 1997; Nicieza & Metcalfe, 1997), environmental factors influencing the body size selection gradients are likely of high evolutionary relevance. The physiological basis for the size-dependency of over-winter survival and the evolutionary consequences in terms of growth rate selection have received considerable attention (reviewed by Conover & Schultz, 1995). However, habitat factors influencing this relationship have largely been neglected (but see Sandlund *et al.*, 1992; Quinn & Peterson, 1996). The present study demonstrates that shelter availability may directly influence the size-dependent energy expenditure and therefore size-related winter survival. Accordingly, reduced habitat complexity may create an environment less favourable for large-sized juveniles and reinforce negative impacts of degradation of stream habitats on salmonid populations.

Although river restoration projects often involve large-scale habitat manipulations, the functional understanding of how the physical structures of the river bed interact with fish performance is unclear. Previous studies have not isolated the effects of habitat structure from the changes in food availability associated with alterations in substrate composition. Also, current methods for assessing substrate quality are based on the size, morphology and distribution of particle sizes. These measures are often tedious to obtain, and as a consequence non-objective visual classifications of substrate quality and embeddedness are often used in management. The present study introduces an efficient and objective measure of substrate quality that is directly related to key features of habitat complexity and salmonid behaviour and physiology. Reduced shelter availability reduces the mean performance of the population and decreases the relative benefits of larger body size. The latter effect may possibly influence the long-term evolutionary processes. Shelter availability is therefore a key habitat factor to consider in habitat assessment and stream restoration aimed at improving conditions for stream living salmonids.

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