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Juvenile salmonid abundance in a diamictic semi-fluvial stream in Norway—does stream bed shelter beat large woody debris?

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Abstract

This study investigates the effect of large woody debris (LWD) on the abundance of juvenile Atlantic salmon (*Salmo salar*, L.) and anadromous brown trout (*Salmo trutta*, L.) in semi-alluvial side channels of the river Aurlandselva (Norway) using point electrofishing and microhabitat mapping. Not the presence of LWD, but stream bed shelter availability and the distance to spawning grounds affected the fish abundance (fish/point), independent of other habitat components. LWD showed only an effect on fish abundance when in interaction with other habitat components. This discrepancy can be explained by the availability of cavities in the shelter-rich coarse substrate which provide sufficient cover and territory for juvenile fish at the given carrying capacity of river Aurlandselva. Whilst LWD may be most effective to provide shelter in lowland streams (bed slope <0.005), maintaining or restoring shelter-rich coarse substrates should be considered a key priority in steeper salmonid rivers and associated semi-fluvial streams.

KEYWORDS
dead wood, fish abundance, fish habitat structure, LWD, river restoration, salmonids, substrate shelter

1 | INTRODUCTION

Dead wood or large woody debris (LWD) is considered an important structural element of streams and rivers, particularly for fishes (Harmon et al., 1986). This is reflected in several projects of stream habitat restoration in which introductions of LWD are applied (Antón et al., 2011; Gerhard & Reich, 2000; Pander & Geist, 2018). The reintroduction of LWD includes a variety of methodologies with which dead trees, branches and roots are put into rivers, with or without anchoring (Forseth et al., 2014; Reich et al., 2003). In addition to the direct use of LWD by fishes as shelter, and analogously to beds of macrophytes and other structural elements, LWD can also change patterns of hydromorphology, substrate sorting and hyporheic quality (Braun et al., 2012) which are crucial for recruitment of gravel-spawning fishes (Smialek et al., 2021; Sternecker et al., 2013). LWD deposits can also create stagnant areas, which are important refugia for fish during floods (Crook & Robertson, 1999). Moreover, dead wood can affect the availability of macroinvertebrates as an important food for salmonids (Jähnig et al., 2009; Ogren & King, 2008).

The placement of wood in running waters is a natural and organic way of influencing the channel dynamics because it is a natural component of every aquatic ecosystem in ecoregions with forests (Kail & Hering, 2005). Several publications point out that especially for fish, dead wood can provide refugia (Keim et al., 2000), and a number of studies showed that dead wood can create attractive habitats for salmonids, with positive effects on fish abundance and other population characteristics (Clark et al., 2019; Crook & Robertson, 1999; Johnson et al., 2005; Slaney et al., 2001). Most studies on salmonids have shown an increase in fish numbers after placing wood (Keller & Swanson, 1979; McMahon & Hartman, 1989; Roni et al., 2014;

Shirvell, 1990; Zika & Peter, 2002), but additional research is needed to comprehensively test the validity of LWD in different stream habitats in relation to other habitat variables. This may be important since types of studied rivers and fish communities have been proposed to be decisive factors for the effects of LWD (Crook & Robertson, 1999; Kail et al., 2007). Also, North American studies about the effects of LWD on fish dominate in the literature, whilst fewer studies have been carried out in Europe (Kail et al., 2007). The least is known about the effects of LWD impacts and their relevance for salmonids regarding the microhabitat in the post-glacial rivers of Northern Europe.

It has been demonstrated that various habitat components, such as living vegetation (Armstrong et al., 2003), flow conditions (Johnson & Douglass, 2009) or suitable sediment cavities ('Finstad-shelter', specifically defined by Finstad et al., 2007), play a significant role in the habitat choice of juvenile Atlantic salmonids. Determining the relative importance of LWD in comparison to these other habitat elements is a crucial aspect of understanding the species' ecology.

The main objective of this study was to assess the effect of LWD, in relation to other habitat factors and distance to spawning grounds, on the juvenile fish abundance of Atlantic salmon (*Salmo salar*, L.) and anadromous brown trout (*Salmo trutta*, L.) within the side channels and branches of a steep Northern European post-glacial river. In line with the large body of studies showing the positive effects of naturally occurring and introduced LWD on fish populations, we hypothesised that the abundance of fish in both species is higher in areas with LWD compared to sites without. Due to the high level of connectivity within the study river system, we also hypothesised that the effect of LWD would be more important in governing the abundance of juvenile fish of both species than other habitat characteristics such as proximity to spawning sites or substrate characteristics.

2 | MATERIALS AND METHODS

2.1 | Study area

This study was performed in four side channels of the river Aurlandselva, in the county of Sogn and Fjordane, Western Norway. The Aurlandselva has a catchment area of 802 km^2 and was once known for its high stocks of sea trout and Atlantic salmon (Jensen et al., 1993; Pulg et al., 2013, 2021). All investigated side channels were located in the lowest river reach, between the river mouth and Lake Vassbygvatnet (53.82 m drop at 7.8 km length, bed slope = 0.007). Since 1969, the discharge regime and sediment transport of the river have been heavily modified by hydropower regulation (Jensen et al., 1993; Væringstad, 2019). The valleys of Aurland are neither strongly afforested nor influenced by agriculture (Pulg et al., 2021; Tyssen, 1991).

The Aurlandselva and its side channels were formed by glaciofluvial processes during and after the melting of the Scandinavian ice shield at the end of the Weichselian glaciation (Hauer & Pulg, 2018). The river exhibits fluvial reaches, semi-fluvial reaches (diamictic and fluvial deposits) and non-fluvial reaches (glacial and colluvial deposits). The side channel morphology corresponds to 'diamictic plane beds' with mud (11.0% coverage), sand (5.4%), gravel (10.9%) and relatively high percentages of the coarser textures cobble (41.0%) and boulders (31.7%). The bed slope of the channels was 0.008. The average Finstad-shelter was 11.8 (weighted shelter). Submerged vegetation was rare and only found in ca. 20% of the area, comprising short-leaved moss (17.2%) and *Callitriche* sp. (8.3%) (Pulg et al., 2021; Ugedal et al., 2019).

Since 2009, intensive efforts of restoration work have been carried out to create new spawning habitats in this river system (Pulg et al., 2021, 2023) by introducing gravel or harrowing the compacted river sediment. In 2012, the side brooks Klekkeribekken (EU89, 60.881825 latitude, 7.244197 longitude) and Tokvamsbekken (60.889203, 7.236981) were restored, mainly by reconnecting them to the main river and by removing small weirs and ground sills as well as planting riparian vegetation and the augmentation of twigs and dead trees in spring 2013 (Pulg et al., 2013). The Klekkeribekken is a 165 m long side channel of the Aurlandselva which was adapted for salmon and trout in September 2012. Before 2012, both the migration of fish and the habitat conditions for the fish were strongly impaired. Restoration works also included an improvement of the substrate through the introduction of gravel and pebbles. Tokvamsbekken is the largest of the side brooks of the lower Aurlandselva, with a length of 875 m. The channel has a water intake at the inlet which is passable for fish. Klekkeribekken and Tokvamsbekken were both restored in the same way. In 2013, throughout the stream edge, dead trees and large branches were laid out fastened with wire and stones. About 50 dead trees/branches with a height of 5–10 m were introduced into both streams. Additionally, two small side channels of the lower Aurlandselva were tested, Onstad 1 & 2 (60.902794, 7.19221; 60.903981, 7.193309) (Figure 1). Both were not part of the restoration programme in 2012–2014 but included a high amount of natural LWD (Figure 2).

2.2 | Field sampling

For improved comparability, all field samplings in this study were conducted within a period of 10 days between 18 October and 28 October 2016. To reduce possible interactions between areas with and without dead wood, each sampling spot was located within defined areas with either a high cover of dead wood (>50%) or no dead wood at all. The sampling points had an area of about 1 m^2 and at least 5 m distance from each other and were randomly chosen. For this study, 85 sampling points were investigated in total, of which 48 contained LWD and 37 did not. Fish abundance is defined as number of fish per sampling point (n/sample point). Originally, different types of LWD/dead wood cover were determined, but not considered for further statistical analysis due to a clear bimodal distribution pattern. The fish assessments were carried out by backpack electrofishing and habitat mapping of sampling points with even distribution. All brooks were probed using the spot sampling electro-fishing method of Riedl and Unfer (2010). For electrofishing, a GeOmega Pulsgenerator with 1400 V and a pulsed current (75 Hz) was used (Pulg et al., 2019). The sampling points were fished by applying the electrical power for a total time of 20 s per site or until no more fish were

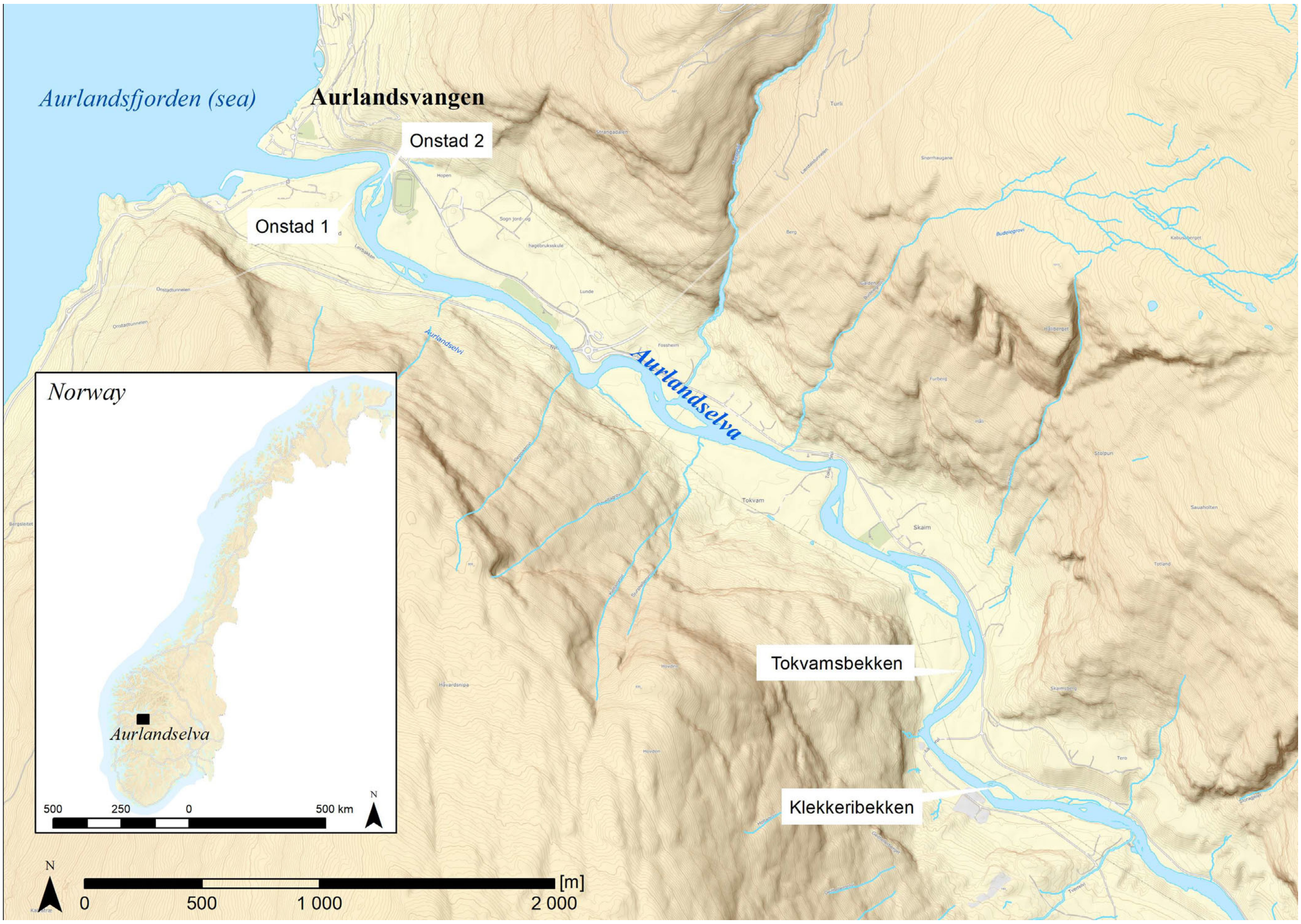

FIGURE 1 Location of the studied side channels at the river Aurlandselva.

FIGURE 2 Introduced LWD in Klekkeribekken (a) and Tokvamsbekken (b), as well as natural LWD (c and d) in two small tributaries in river Aurlandselva.

observed. Sampled fish were identified, counted and their individual total lengths (TL) measured to the nearest mm. Observed salmonids escaping the electric field from the sampling spot were also registered, distinguished between parr and fry and included in the fish abundance data.

After completion of the electrofishing, the habitat was mapped, and the abiotic parameters of the spots were sampled. The habitat mapping comprised a habitat structure characterisation, whereby LWD, vegetation, shelter, substrate, flow velocity and variance, as well as depth, were chosen as relevant habitat variables (Riedl & Unfer, 2010). Additionally, the data for the variable spawning grounds were created with already existing spawning ground mapping data material provided by the 'Laboratory for Fresh water ecology and inland fisheries' (LFI, Pulg et al., 2023). The presence/absence, type of LWD and estimated cover were recorded for every sampling point ($\sim$1 m^2). The sampling points 'with LWD' contained wood impacts that were fixed by 'hard engineering' (Kail et al., 2007), but they also had areas with non-fixed wood structures. The vegetation coverage at every sampling point was estimated in percent by a person with a diving suit and snorkel equipment. The type of vegetation was described and classified as 'submersed aquatic plants', 'algae and/or moss' or 'various'. Shelter for juvenile fish in the form of interstitial spaces between cobbles or amongst twigs, roots and vegetation was measured using the method of Finstad et al. (2007) and Forseth et al. (2014). The variable used is 'weighted shelter' (WS, Finstad et al., 2007).

The numbers and dimensions of interstitial spaces suitable as a shelter for juvenile salmonids were characterised following the methodology by Forseth et al. (2014). Briefly, we quantified how many times a 13 mm thick plastic hose could be inserted into holes between stones within areas of a 0.25 m^2 steel frame based on two replications per individual sampling point. The sizes of interstitial spaces were determined based on how far down between the stones the hose could be inserted. Three shelter categories were assigned: S1: 2–5 cm, S2: 5–10 cm and S3: >10 cm.

The substrate class relations of the chosen patches were estimated visually in percent (in 5% steps) by underwater mapping. Following the procedures outlined by Forseth et al. (2014), the substrate was categorised into four classes specifically adapted to salmon habitat requirements: (1) silt, sand and fine gravel (<2 cm); (2) gravel and pebble (2–12 cm); (3) cobble (12–29 cm) and (4) boulders (≥30 cm). Classified substrate mapping (Forseth et al., 2014) at the tested 85 sample points showed that gravel and pebble made up the highest amount of the sediment (35 ± 23%), followed by cobble (31 ± 18%) and silt, sand and fine gravel (21 ± 24%). Boulders made up the smallest amount (13 ± 17%) at the tested sampling points.

The flow velocity and variances of the flow rate were measured (Valeport Model 810 cylindrical EM Flow Meter) by measurements directly on the riverbed and additionally at 40% of the total depth from the bottom. Flow data and total depth (in centimeter) were consistently measured at the centre of each sampling point. Data for the spawning sites were provided by the LFI and were mapped between 2012 and 2015 (Pulg et al., 2021; Ugedal et al., 2019). The distance to the spawning sites was measured with ArcMap (Arc Gis 10.5, ESRI 2016). The measurement tool in ArcMap was used to determine the distance between the GPS location of each site and the closest spawning bank (both upstream and downstream). At every stream, the temperature and conductivity were measured with a handhold logger (WTW multi 3640) before taking the fish samples. If there was organic material, leaves, boulders or riprap, this was noted, too. For the data analysis, both species of Atlantic salmon and anadromous brown trout were pooled as 'Atlantic salmonids' (Foldvik et al., 2017; Pulg et al., 2019), because of the similar habitat requirements and overlap of habitat (Armstrong et al., 2003; Heggenes et al., 1999).

2.3 | Data analysis

The substrate categories were reclassified into four categories based on salmon habitat requirements, and the 'substrate weighting' (SW) was then calculated using an adapted formula according to Forseth et al. (2014). Category 1 refers to substrate 'generally unsuitable' for salmonids and is not weighted in the formula (compare also Suttle et al., 2004). Category 2 is 'suitable for spawning', which implies more shelter for 0+ fish, with an assigned weighting of 1. Categories 3 and 4 are considered ideal for parr of various sizes and are therefore assigned the highest (2) score. SW was calculated according to the following formula:

$$\mathrm{SW} = (\mathrm{category}\,1 \times 0 + \mathrm{category}\,2 \times 1 + \mathrm{category}\,3 \times 2 + \mathrm{category}\,4 \times 2)/100.$$

The shelter availability was quantified as WS. For the analysis, the average of the number of shelter categories was calculated when two shelter measurements were performed. Finally, the values were summed up with the formula:

$$\mathrm{WS} = \mathrm{S1} + \mathrm{S2} \times 2 + \mathrm{S3} \times 3.$$

To reflect the general shelter quality in the streams the WS classes were assigned to 'low shelter' (<5), 'moderate shelter' (5–10) or 'high shelter' (>10) (Forseth et al., 2014). For all data interaction analyses of fish abundance and shelter, the WS data were not categorised.

Collected data were tested for normality by applying Kolmogorov–Smirnov tests (KS test). To assess the potential impact of LWD on fish abundance within the context of all other habitat variables and to ascertain the respective contributions of each habitat variable to fish abundance, we conducted a multilinear regression model. Links between the independent variables with the juvenile salmonid abundance were tested using Spearman Tests (substrate composition (WS), substrate shelter (SW), flow velocities, flow variances and spawning ground distances) or Mann–Whitney *U* tests (vegetation). To test whether sampling points with and without LWD differed in fish abundance and fish length frequencies, Mann–Whitney *U* tests were applied. As substrate and LWD were assumed to be related to shelter, Spearman tests were used to test their relationship, with shelter as a dependent variable.

As this bivariate analysis identified a strong relationship between shelter and fish abundance, whilst there was no sufficient statistical evidence in the impact of LWD, linear and multilinear regression was applied to test the interaction between LWD, shelter and fish abundance. To assess the potential impact of LWD on fish abundance within the context of all other habitat variables and to ascertain the respective contributions of each habitat variable to fish abundance, we applied a multilinear regression model. This full model analysis encompassed all habitat variables, along with an interaction term derived from LWD and substrate shelter data. Only the nearest spawning ground data were used in the model, since this involves both spawning grounds upstream and downstream and it was shown to have a statistically significant effect and a substantial magnitude of effect size on fish abundance. Input data for the model were normalised (divided by the mean value). Results are presented as arithmetic means ± standard deviation. All statistical analyses were carried out using SPSS (IBM SPSS Statistics 24, SPSS Inc., Chicago, Illinois, USA) and Microsoft Excel 2016. Significance was accepted at $p < 0.05$.

3 | RESULTS

In total, 165 fish were counted during electrofishing, of which 63.6% (105) were juvenile brown trout and 16.4% (27) were juvenile Atlantic salmon. 20.0% (33) were observed but not caught and were considered unidentified salmonids. Total length of 105 measured trout ranged from 39 to 230 mm with a mean length of 89.5 ± 37.4 mm (Figure 3). The 27 measured salmon ranged from 41 to 140 mm with a mean total length of 69.4 ± 28.9 mm. There were no statistically significant differences in fish mean lengths between sampling points with and without the presence of LWD (Whitney *U* test, $U_{52,80} = 1913.5$, $p = 0.438$, mean ranks: 63.30 and 68.58).

Sites including LWD contained 2.06 ± 1.66 fish, whilst sites without LWD had a lower fish abundance of 1.78 ± 1.47 fish per sample point (Figure 4). In approximately 20% of the sample points, no fish were observed. Only a few sampling points contained ≥4 fish. On both sites including LWD and sites without LWD more parr than fry were found (Figure 5).

Sampling points with and without LWD showed no significant difference in fish abundance (Whitney *U* test, $U_{37,48} = 806.0$, $p = 0.457$; mean ranks: 40.78 and 44.71). A linear regression using LWD as a binary dummy variable and fish abundance as a dependent variable was also not significant ($t = 3.019$; $p = 0.457$). Shelter values were significantly smaller in the presence of LWD (Whitney *U* test, $U_{37,48} = 660.0$, $p < 0.05$, mean ranks: 49.16 and 38.71) (Figure 4). There was a significant positive correlation between shelter and fish abundance (Spearman, $r_s = 0.248$, $p = 0.022$, $n = 85$) (Figure 6). A multilinear regression ($F(2,82) = 6.023$, $p = 0.004$) between shelter and LWD and the fish abundance showed a significant positive correlation between shelter and fish abundance ($t = 3.364$, $p = 0.001$). In contrast, there was no significant correlation between LWD and fish abundance ($t = 1.655$, $p = 0.1$). A Spearman test between substrate weighting and shelter showed a statistically significant and positive rank-order correlation between these variables ($r_s = 0.602$, $p < 0.001$, $n = 85$). When the shelter values were assigned to classes after Forseth et al. (2014), 36 of all sampling points were classified as 'low shelter' (42.4%), 24 sampling points as 'moderate shelter' (28.2%), and 25 sampling points as 'high shelter' (29.4%).

The sample points had different distances to the spawning sites. Six sample points were directly on the spawning sites, whilst the rest

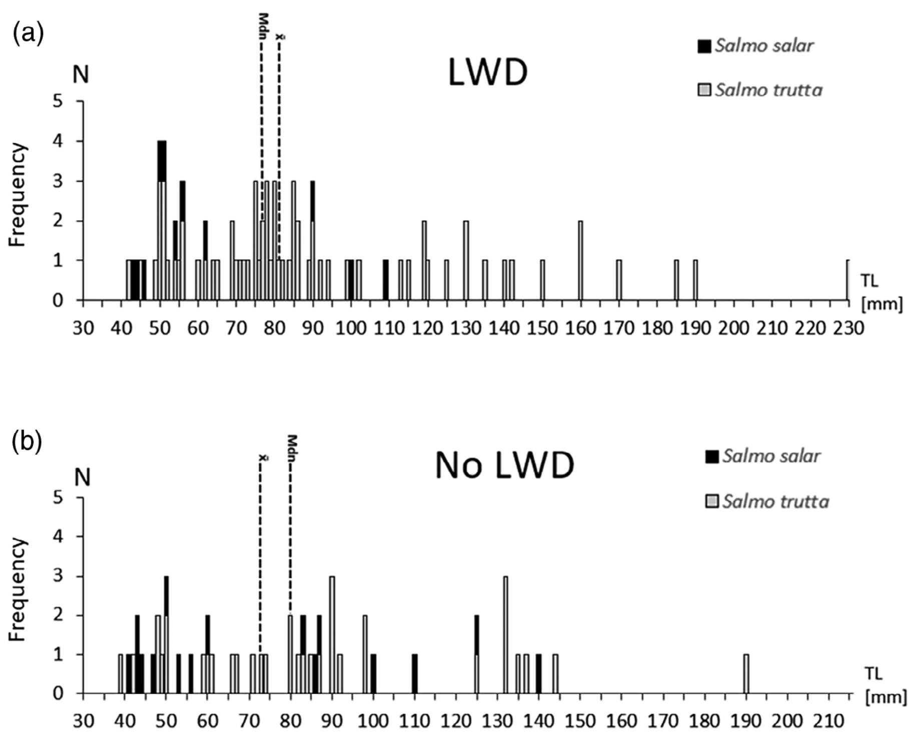

FIGURE 3 Length frequency distribution of all measured *Salmo trutta* ($N = 105$) and *Salmo salar* ($N = 27$) on sites with (a) presence ($N = 48$) and (b) absence ($N = 37$) of LWD. Observed fish are excluded. The grey dashed line represents the mean length ($\bar{x}$) and the black dashed line is the median length (Mdn) of all sampled fish.

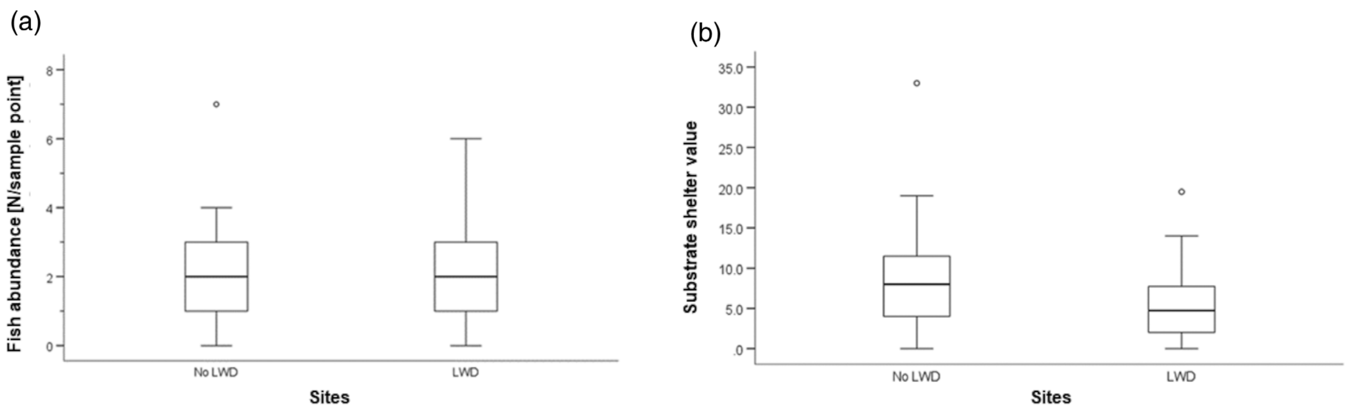

FIGURE 4 (a) Mean fish abundance and (b) weighted shelter results of sampling points including LWD ($N = 48$) and without LWD ($N = 37$). Sites without LWD provided significantly more shelter (Spearman, $r_s = 0.602$, $p < 0.001$, $n = 85$).

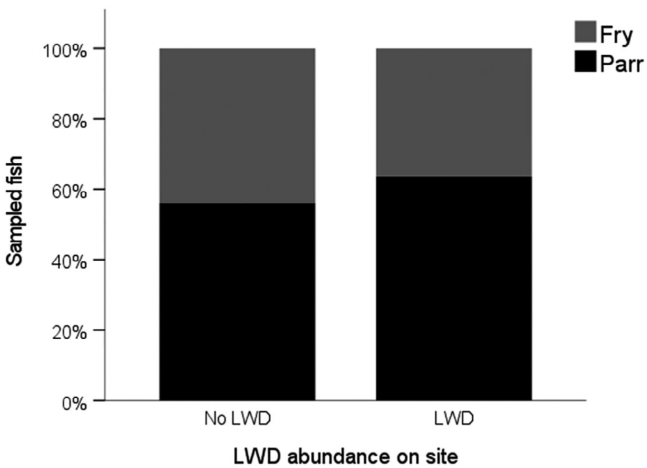

FIGURE 5 Proportion of fry and parr of all sampled fish on sites with ($N = 99$) and without LWD ($N = 66$).

were up to 97 m away from the nearest spawning ground (Table 1). There was a negative statistically significant correlation between the nearest spawning grounds and the fish abundance ($r_s = -0.229$, $p = 0.036$, $n = 84$) and the nearest spawning ground upstream and fish abundance ($r_s = -0.272$, $p = 0.012$, $n = 84$) (Figure 7). Increasing distance between the spawning areas from the measuring points was inversely related to fish abundance. There was no significant correlation between the spawning sites downstream and fish abundance ($r_s = -0.108$, $p = 0.327$, $n = 84$).

The full multilinear regression model including all habitat variables showed that shelter ($t = 5.089$, $p < 0.001$) and LWD ($t = 2.326$, $p = 0.023$) had a positive effect on the fish densities (Table 2). Distance to the nearest spawning ground was negatively correlated to fish abundance with increasing distance ($t = -3.844$, $p < 0.001$). The interaction between shelter and LWD had a significant influence on fish abundance, with a negative regression coefficient. This suggests that the presence of LWD reduces the overall effectiveness of shelter in supporting fish abundance, decreasing from 0.658 to 0.267 (a reduction of 0.391) ($t = -2.142$, $p = 0.036$). The variables vegetation, flow velocity and variance, substrate and depth were not significantly correlated with the fish abundance in any models. Water temperature was similar among all sampled brooks (5.9–6.1°C).

4 | DISCUSSION

Juvenile fish abundance was correlated to shelter availability and distance to spawning habitats, but not to the presence of LWD. This result runs contrary to the findings of many other studies that have shown a positive effect of LWD on the abundance of salmonids (Degerman et al., 2004; Roni & Quinn, 2001; Thompson et al., 2018; Zika & Peter, 2002), albeit in different stream types. However, a few studies also observe no LWD-fish relations: Riksfjord (2014) studied the effect of woody debris on juvenile trout abundance and biomass in the Foldvik- and Bjønnes streams in Western Norway and did not detect a positive effect.

Atlantic salmon and brown trout juveniles depend on both cover and shelter (Armstrong et al., 2003; Finstad et al., 2009; Jonsson & Jonsson, 2011) which they find either in the cavity of coarse sediment or near living and dead vegetation. On the other hand, fish abundance is also limited by the carrying capacity of the stream as determined by the amount of food. Under more eutrophic conditions and in-stream systems providing little structural richness and limited shelter, effects of LWD would be expected to be stronger compared to the oligotrophic stream system with high stream bed shelter investigated herein. Consequently, the observed discrepancies amongst studies about the effects of LWD can be explained.

The strong linkage of LWD and fish abundance in many studies points to LWD as the main factor offering shelter and cover in these rivers. This is likely the case in rivers with a fluvial morphology, sorted gravel, fine gravel or sand where LWD and plants are the only coarse substrate offering cavities big enough for fishes over 4 cm. In semi-fluvial rivers with diamictic sediments as well as in steeper rivers (>0.005 bed slope) with coarser sediment such as pebble, cobble and boulders, cavities in the sediment offer plenty of shelter and habitat for the territorial juveniles (Finstad et al., 2007; Hauer & Pulg, 2018;

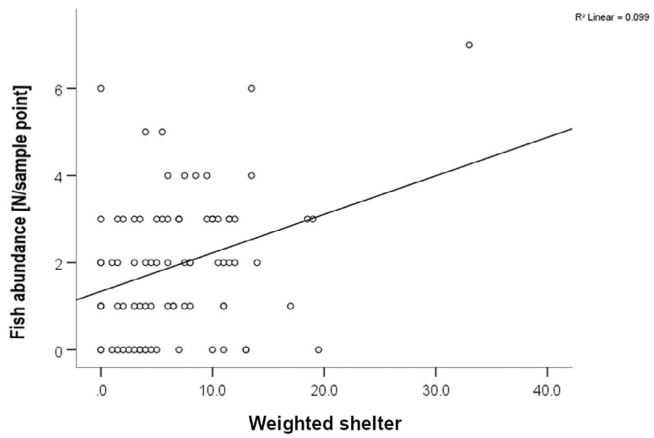

FIGURE 6 Abundance of fish ($N = 165$) and measured substrate shelter parameters correlated significantly (Spearman, $r_s = 0.248$, $p = 0.022$, $n = 85$).

TABLE 1 Measured habitat variables of 85 sampling points in the river Aurlandselva.

Variable	Min	Max	Mean	SD
Shelter (WS)	0.00	33.00	6.80	5.60
Depth (cm)	9.00	80.0	29.20	11.70
Flow 0 (m/s)	−0.24	0.60	0.08	0.13
Flow variance 0 (m/s)	0.01	0.32	0.04	0.04
Flow (m/s)	−0.10	0.88	0.14	0.18
Flow variance 40 (m/s)	0.00	0.86	0.05	0.11
Vegetation cover (%)	0.00	90.00	10.00	16.60
Substrate weighting (SW)	1.00	20.5	12.41	4.10
Nearest Spawning ground (m)	0.00	97.00	21.13	26.70
Nearest Spawning ground upstream(m)	0.00	138.00	34.92	37.47
Nearest Spawning ground downstream (m)	0.00	174.00	37.26	52.65

Note: Flow 0 and Flow variance 0 were measured directly on the riverbed; Flow 40 and Flow variance 40 were measured at 40% of the total depth from the bottom. Flow data and total depth (cm) were always measured at the centre of the sampling point. Substrate weighting was classified with an adapted formula according to the substrate classification of Forseth et al. (2014). It indicates a suitable substrate with increasing value for parr of various sizes.

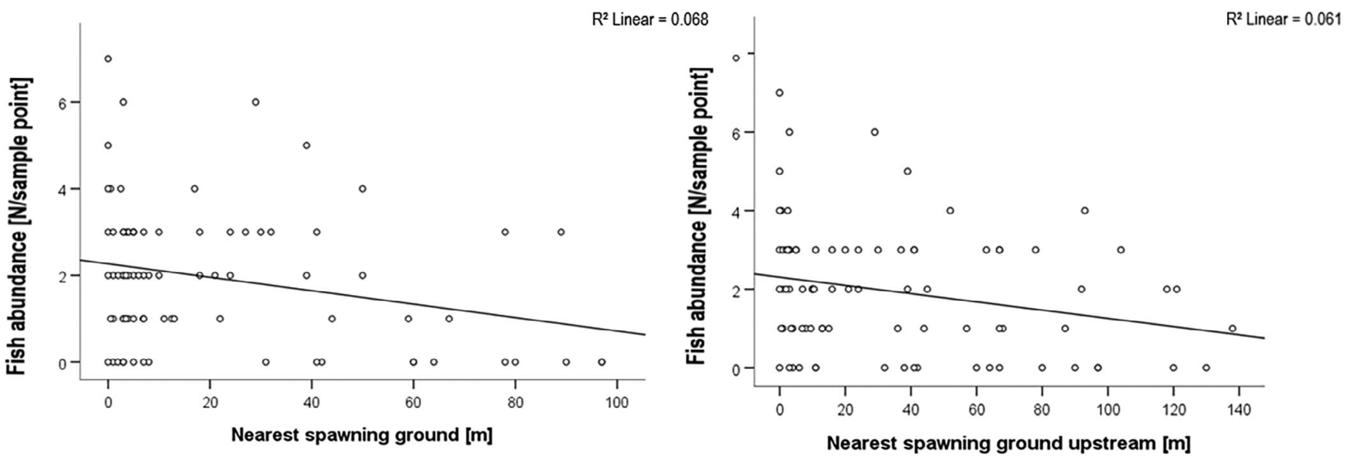

FIGURE 7 Association between the abundance of fish ($N = 165$) and distance to the nearest spawning ground (left) and nearest spawning ground upstream (right). The nearest spawning ground (*Spearman*, $r_s = -0.229$, $p = 0.036$, $n = 84$) and nearest spawning ground upstream (Spearman, $r_s = -0.272$, $p = 0.012$, $n = 84$) correlated significantly with the fish abundance. The closer the spawning site, the higher the abundance of juvenile fish.

TABLE 2 The multilinear regression model with Fish abundance as the dependent variable, including the variables Shelter, LWD, Depth, 'Substrate weightening', Flow velocity 0, Flow variance 0, Flow velocity 40, Flow variance 40, Vegetation, Spawning ground (nearest) and a variable called Interact_Shelter_LWD (multiplied Shelter and LWD values).

		Unstandardised coefficients		Standardised coefficients		
Model		B	Beta	Beta	*T*	Sig.
1	(constant)	0.966	0.466		2.073	0.042
	Shelter (WS)	0.648	0.127	0.658	5.089	<0.001
	Flow velocity 0	−0.086	0.083	−0.167	−1.047	0.299
	Flow variance 0	−0.085	0.076	−0.121	−1.120	0.266
	Flow velocity 40	−0.075	0.110	−0.112	−0.678	0.500
	Flow variance 40	0.028	0.045	0.072	0.620	0.537
	Depth	−0.324	0.213	−0.159	−1.517	0.134
	Substrate (SW)	−0.031	0.322	−0.013	−0.097	0.923
	LWD	0.678	0.291	0.416	2.326	0.023
	Vegetation	0.118	0.169	0.073	0.699	0.487
	SP_nearest	−0.257	0.067	−0.398	−3.844	<0.001
	Interact_Shelter_LWD	−0.233	0.109	−0.391	−2.142	0.036

Pulg et al., 2019). The reason why no strong linkage was found between fish abundance and LWD in our study and similar rivers of Scandinavia (Riksfjord, 2014) can thus be explained by the high shelter availability of the diamictic coarse sediment in the rivers researched in which the fish did not depend on the additional shelter provided by LWD. Contrary to these findings, Degerman et al. (2004) and Donadi et al. (2019) discovered discrepant results based on data from a wider variety of stream types in Sweden. This broader range of stream types may have contributed to stronger associations between LWD and fish abundance in these studies, and direct shelter in the substrate was not considered the same way. Recent evidence also suggests that excess fine sediment introductions resulting in colmation and poor stream bed quality can be a limiting factor for recruitment of freshwater pearl mussels and their salmonid hosts in Sweden, with restoration of greater exchange rates between open water and the interstitial zone of the stream bed (e.g., by substrate raking or introduction of LWD) improving habitat quality (Geist et al., 2023). Given the potential significance of shelter in habitat choice, we emphasise the need for future data analysis to explicitly incorporate substrate shelter as a critical factor in the models. To check if the correlation between substrate shelter and fish abundance may be driven by an extreme sampling point with the highest substrate shelter and fish abundance (Figure 5), it was tested with and without this data point. The correlation without this sampling point was only slightly weakened but still showed the same trend and statistical significance (Spearman, $r_s = 0.220$, $p = 0.045$, $n = 84$).

River morphology type and sediment composition may help to understand to which degree LWD impacts fish abundance. Crook and Robertson (1999) discussed different LWD effects in different river types, with lower effectivity of LWD in alpine coarse gravel bed rivers and higher effectivity in sand-dominated lowland rivers. Substrate shelter availability in fluvial rivers with finer (≤gravel) and sorted, non-diamictic sediments is lower than in semi-fluvial rivers with diamictic sediment or fluvial rivers with coarser substrate (dominated by pebble, Hauer & Pulg, 2018). The genesis of rivers and their morphology should be considered when planning restoration and habitat enhancement measures (Hauer & Pulg, 2021). When aiming at increasing shelter for Atlantic salmon and brown trout, it is therefore suggested to prioritise LWD in low gradient (<0.005), fluvial rivers with sorted gravel sediment or finer sediments. The same principle also holds true for highly modified lowland rivers with lower slopes, where LWD was shown to be widely accepted by a diverse fish community (Pander & Geist, 2018). In steeper rivers with shelter-rich sediments such as non-clogged pebbles or small boulders as well as in semi-fluvial rivers with diamictic sediment composition, LWD input may be less effective for providing shelter.

Other known LWD effects such as an increase in insect availability (Ogren & King, 2008; Thompson et al., 2018) may have existed at our study site but could not be detected by the sampling methods (especially if predation by fish is not actively excluded) and scale chosen. Drifting insects from LWD may also consume fish several metres downstream in the shelter-rich substrate of a non-LWD site and may thus have affected fish abundance on both LWD and non-LWD sites.

A suitable substrate type does not always imply that interstitial shelter is available. The results show a significant correlation between shelter and the substrate, but the substrate type was not linked to the number of fish. This can be explained by the deposition of fine sediment (Finstad et al., 2007), but also by very similar sediment conditions, indicating that cavity is a better predictor for fish abundance than substrate type.

Bankside, submerged or overhanging vegetation is considered to play a crucial role in habitat and shelter provisioning for juvenile salmonids (Armstrong et al., 2003; Maki-Petäys et al., 1997; O'grady M., 1993; Roussel et al., 1999), but depending on the channel width, it can also result in shading and decreased primary production within the stream itself. In our data, no effect of aquatic vegetation on fish abundance was observed. A reason for this result could be that the vegetation was dominated by small mosses (1–3 cm), which do not provide shelter for the size of juvenile fish found in this study.

The correlation between juvenile abundance to the nearest spawning site is well described in the literature (Teichert et al., 2011), both for fry and parr (Pulg et al., 2019, 2021) and was also observed in our dataset. As expected, spawning sites upstream had a positive effect on fish abundance (Gustafson-Greenwood & Moring, 1990; Johnston, 1997). The further the distance of spawning areas to the sampling points, the less fish were captured, confirming assumptions according to Gustafson-Greenwood and Moring (1990), clearly indicating that the spawning places influence the abundance of fish. Several studies show that woody debris are just one component of shelter and suitability for salmonids in their habitat (Aas et al., 2010; Armstrong et al., 2003; Riedl & Unfer, 2010). It can be fallacious to judge habitat selection from the effect of a single factor alone (Jonsson & Jonsson, 2011). Altogether, depth, current, substrate and cover are the most important habitat features determining the distribution and abundance of salmonids (Heggenes, 1990; Heggenes & Saltveit, 1990). Further, uninvestigated factors such as food availability, but also species-specific differences could have affected the results as well. Analogously to earlier studies (Foldvik et al., 2017; Pulg et al., 2019), we pooled brown trout and Atlantic salmon as Atlantic salmonids, to ensure a sufficient sample size for robust statistical analyses and to also include those specimens that were only observed but could not be determined to species level. According to Jonsson and Jonsson (2011), brown trout are more dependent on suitable overhead cover (such as stones, riparian vegetation or LWD) than Atlantic salmon. Results from another Swedish study indicate that LWD can serve as a valuable means for restoring brown trout populations in shallow and confined streams, particularly in regions with limited shade (Donadi et al., 2019). In their findings, the presence of LWD positively impacted the abundance of juvenile brown trout but had no discernible effect on the abundance of Atlantic salmon, with the beneficial influence of LW abundance on trout being more pronounced in less shaded locations. In our study, only a small number of Atlantic salmon were caught, mirroring as well that juvenile trout abundances are higher than those of Atlantic salmon in Aurlandselva (Pulg et al., 2021). However, species-specific differences should be addressed appropriately in future studies. The small sampling numbers are also reflected in general weak correlation factors in our models (Table 2). Furthermore, the observations in Aurlandselva are only based on side channels of one river reach and one river type (diamictic plane bed). We therefore stress the need for further studies and recommend increasing the sample size.

Considering these limitations, and in conjunction with evidence given in the literature, we conclude that the shelter effect of LWD is likely to be limited in rivers with high shelter availability in the sediment. For the juvenile fish, the cavities in the shelter-rich coarse substrate provided enough cover and territory, which makes the abundance of LWD less relevant. This is an important point regarding the cost and benefits of various habitat restoration approaches, which can help to prioritise the limited funds available to fish population recovery efforts. However, besides the shelter-aspect, it is essential to acknowledge that LWD introduction may indeed provide additional benefits for fish in riverine ecosystems, since it has the potential to increase habitat diversity and the availability of food resources and energy inputs, contributing to enhanced carrying capacity, even in rivers with abundant substrate cavities (Harvey et al., 2018; Thompson et al., 2018). Therefore, categorically discouraging the supply of LWD in such rivers is not advisable, especially when it is part of the given environmental setting. Hence, the restoration should be adapted to the local conditions based on the characterisation of habitats (Geist & Hawkins, 2016), natural processes and local river morphology (Beechie et al., 2010; Hauer & Pulg, 2021). In the case of the Aurlandselva and other post-glacial Western Norwegian rivers with similar morphology, bed slope and coarse semi-fluvial sediments, the availability of substrate shelter (sediment management or sediment loosening) may be prioritised over dead wood input when aiming at increasing shelter availability (Pulg et al., 2018). LWD augmentation may be the preferred shelter-measure in streams with lower bed slopes (<0.005) and fluvially sorted gravel, sand or silt.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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