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Large woody debris and brown trout in small forest streams – towards targets for assessment and management of riparian landscapes

Erik Degerman, Berit Sers, Johan Törnblom and Per Angelstam

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Large woody debris (LWD) was quantified in 4382 forest stream sites in Sweden. LWD was present at 73% of the sites, but the amount was low with a median number of 1 piece of LWD 100 m^{-2}. Brown trout was the most frequently occurring fish species and occurred in 82% of the sites. Brown trout occurred more frequently in sites with LWD, and the abundance of trout increased with the amount of LWD up to 8–16 wood pieces 100 m^{-2}. By using quantity of LWD and stream width, brown trout abundance could be partly predicted. The largest trout caught were significantly larger at sites with LWD present, with an average of 188 mm in sites without LWD and 200 mm in sites with LWD. The average size of juvenile fish <1 yr old was 6% lower at sites with >4 pieces of LWD then at sites without LWD. This is suggested to be caused by higher trout densities with increasing amount of LWD, i.e. implying a density-dependent effect on growth.
The relationships between LWD and brown trout suggest that both are useful indicators of intactness and functionality of streams. However, we neither know what the absolute amount of dead wood and trout would be in naturally dynamic riparian landscapes, nor the extent to which brown trout indicates other elements of biodiversity in streams. Our study supports the growing insight that there are complex interactions between terrestrial and aquatic systems. We discuss the need for transdisciplinary landscape scale approaches, such as developing assessment tools for aquatic landscapes in parallel to for example terrestrial gap analyses of habitat structures that maintain biodiversity.

E. Degerman (erik.degerman@fiskeriverket.se) and B. Sers, National Board of Fisheries, SE-702 15 Örebro, Sweden. – J. Törnblom, Dept of Natural Sciences, Centre for Landscape Ecology, Örebro Univ., SE-701 82 Örebro, Sweden. – P. Angelstam, School for Forest Engineers, Fac. of Forest Sciences, Swedish Univ. of Agricultural Sciences, SE-739 21 Skinnskatteberg, Sweden and Dept of Natural Sciences, Centre for Landscape Ecology, Örebro Univ., SE-701 82 Örebro, Sweden.

Lotic and lentic systems are closely connected to the terrestrial environment, which provides resources that are essential to their integrity (Karr and Chu 1999). The aquatic-terrestrial interface itself is a porous filter that allows a flow of organisms, water, and matter in both directions. This interface is often a special habitat with its own unique flora and fauna that contributes significantly to the function of the surrounding landscape. Despite their highly dynamic nature, intact riparian landscapes provide predictable ecological conditions at local and landscape scales (Karr 2000). A challenge for the future is to more rigorously quantify links between pattern and process, as well as to investigate the mechanistic relationships between landscape diversity and species diversity (Ward et al. 2002).

The production of fish and invertebrates in forest streams is naturally based on the riparian forest supply of organic matter and nutrients, and dimensioned by the riparian forest regulation of stream flow, temperature, insolation and sediment load. The riparian forest also supplies large woody debris (LWD) to forest streams. Several studies, especially in the U.S. coastal Pacific Northwest, have demonstrated the effect of large woody debris on the habitat and hydrodynamics of forest streams. LWD can affect channel morphology by flow deflection sometimes creating scour pools, decreasing distance between pools (Beechie and Sibley 1997), increasing total pool area (Roni and Quinn 2001) and in some instances by reducing flow and thus increasing the deposition of fine sediments and debris (Wallace et al. 1995). This leads to increased nutrient retention in the streams (Valett et al. 2002). Further, the stream banks and channel are stabilized (Tschaplinski and Hartman 1983) and the habitat diversity increases (Naiman et al. 1992).

Large woody debris is important for salmonid production, mainly due to increased habitat diversity (Fausch and Northcote 1992, Flebbe and Dolloff 1995). Studies have shown that artificial addition of LWD will increase salmonid density and biomass (Flebbe 1999, Roni and Quinn 2001, Lehane et al. 2002), as well as individual growth (Sundbaum and Näslund 1998). According to Murphy and Koski (1989), 90% of the large woody debris in the water is associated with the nearest 30 m of the riparian zone. This indicates that the riparian zone even in small streams is of essential importance not only to fish densities but also to retention capacity and stream morphology.

Historically, the amount and quality of LWD in streams has not been studied as well as in terrestrial forest systems. Few studies on LWD exist for Scandinavian streams (Bergquist 1999, Siitonen 2001). However, some evidence suggests large declines of LWD compared with the natural range of variability as in terrestrial environments. Many streams have been cleaned of LWD prior to log driving and for pure drainage reasons, but these actions do not alone explain the last 40 yr situation with a continuing low supply of LWD to Scandinavian streams. Lazdinis and Angelstam (in press) quantified the amount of riparian forest in Sweden and the former Soviet Union having different policies for the management of forests along streams. They found that old forest did not exist along the selected Swedish streams, whereas due to policies in the former Soviet Union demanding riparian corridors an average of 20% the forests along streams was old-growth with continuous production of dead wood. Enetjärn and Birkö (1998) and Liljaniemi et al. (2002) found that the abundance of coarse woody debris (CWD) was 10- to 100-fold higher in reference streams in boreal forest in Russia compared with Swedish and Finnish streams, respectively, in managed boreal forests. It has been suggested that LWD could be a factor limiting trout populations on a large scale in Sweden (Näslund 1999). Indeed, Inoue and Nakano (1998) noted that density of Masu salmon *Oncorhychus masou* was directly correlated with the amount of woody debris.

The purpose of the present study is to test the hypothesis that there exists a positive correlation between occurrence and abundance of brown trout *Salmo trutta* and quantity of LWD in Swedish streams. Should this be the case, it would be possible to relate the level of human disturbance in the terrestrial environment to the amount of different elements of biodiversity in the aquatic environment. This could also encourage the development of tools analogous to the gap analyses for assessment of the amount of different vegetation types needed to maintain biodiversity (e.g. Angelstam and Andersson 2001, Lõhmus et al. 2004). Similarly, it would allow the use of habitat models for proactive planning of representative and functional habitat networks being based on focal species representing vegetation types with gaps (Scott et al. 2002, Angelstam et al. 2004). Hence, using quantitative knowledge about specialised aquatic focal species, such as trout, assessment and planning tools based on quantitative targets for habitat structures like LWD could be developed.

Material and methods

Data on LWD and fish were compiled from the Swedish Electrofishing RegiSter (SERS), a database with over 10 000 studied sites in Swedish streams. To date, LWD has been quantified at 4382 forest stream sites. Only sites in forest, i.e., with riparian zones (15 m wide zone adjoining the stream according to Swedish Electrofishing Field Manual (Degerman and Sers 1999)) classified as coniferous, deciduous or mixed forest, were included. The sites were located at altitudes of 1–895 m a.s.l. (average 175 m a.s.l).

LWD was defined as having a diameter of 10 cm or more and a length of at least 50 cm. The number of pieces of LWD was counted in the site and presented as pieces of LWD 100 m^{-2}.

The sampling sites were normally selected in areas of the streams with a habitat suitable for spawning and the first years of growth of brown trout (i.e. riffle-run habitats). Electrofishing was carried out in August–September by wading, using dead or pulsed dead electric current. The average length of stream sampled was 46.8 m (SD=25), the average width was 6.8 m (SD=10) and the average sampled stream area was 238 m^2 (SD=208 m^2).

Fish were measured (total length), and determined to species, but not sexed or aged. Underyearlings, 0+, were separated from older trout using length frequencies and treated separately in density estimates. Population densities were estimated according to Bohlin et al. (1979) if consecutive runs had been carried out. Otherwise densities were estimated from average catch efficiencies for the species and age group (Degerman and Sers 1999).

Environmental variables registered were: width, mean depth, maximum depth, dominating and sub-dominating substrate. The substrate was classified in five categories (1–5) based on the dominant particle size: <0.0002 m (fine=1), 0.0002–0.002 m (sand=2), 0.002–0.02 m (gravel=3), 0.02–0.2 m (stone=4) and >0.2 m (boulder=5). Water velocity was classified into three classes: <0.2 m s^{-1} (1), 0.2–0.7 m s^{-1} (2), >0.7 m s^{-1} (3) at sampling, i.e. late summer flow situation. From maps the size of the catchments and the proportion (%) of lakes within the catchment were measured. Due to skewed distributions, fish abundance and stream width were transformed using $\log_{10}$ to avoid significant deviation from a normal distribution when performing statistical analysis. The amount of LWD was divided into three groups in most analyses: 0 pieces 100 m^{-2}, >0–4 pieces 100 m^{-2} and >4 pieces 100 m^{-2}. Also, stream width was in some analyses used as a grouped variable: <4 m, 4–8 m and >8 m.

Results

Trout occurrence

Brown trout was the most frequently occurring fish species in the investigated sites and occurred in 82% of the sites. Along with trout, seven fish taxa occurred at >10% of fishing occasions: bullheads (*Cottus gobio* and *C. poecilopus*), minnow *Phoxinus phoxinus*, burbot *Lota lota*, pike *Esox lucius*, brook lamprey *Lampetra planeri*, Atlantic salmon *Salmo salar* and perch *Perca fluviatilis* (Table 1).

LWD was present at 73% of sites. Brown trout occurred more frequently at sites with than at sites without LWD (Fig. 1, Anova with absence/presence of LWD and three stream width classes, p<0.001, n=4109, the interaction of LWD and width not significant).

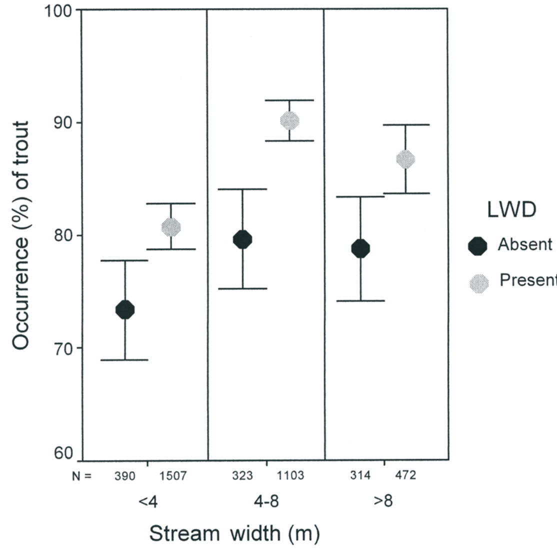

Fig. 1. Proportion (%) of sites with brown trout versus stream width class and presence/absence of Large Woody Debris (LWD). Bars indicate 95% confidence intervals.

Abundance

The abundance of trout increased with LWD (Fig. 2). This was especially pronounced in sites with > 4 pieces of LWD 100 m^{-2} and in larger streams (Anova, $\log_{10}$ abundance 100 m^{-2} with LWD-class (n=3) and width class (n=3) as fixed factors, p<0.001, r^2=0.190, n=3409). In fact, the abundance of trout increased with increasing amount of LWD up to 8–16 pieces 100 m^{-2} (Fig. 3). Using quantity of LWD and stream width, brown trout abundance could be predicted (linear regression, all variables transformed using $\log_{10}$, r^2=0.21, p<0.001).

Size of trout

Maximum size of the trout caught at each site was correlated with LWD. The largest trout caught averaged 188 mm

Table 1. The most frequently occurring taxa at the investigated sites (n=4382). The estimated abundance was calculated only for occasions when the species was caught (i.e. 0 is not included).

Species and taxa	Frequency (%)	Frequency (n)	Abundance 100 m^{-2} Average (SD)	Abundance 100 m^{-2} Median
Brown trout	82.4	3609	32.0 (50.5)	15.3
Bullheads	33.3	1461	24.4 (38.4)	11.6
Minnow	30.1	1318	23.9 (63.4)	5.8
Burbot	22.3	1007	2.9 (5.4)	1.3
Pike	18.2	796	1.4 (1.8)	0.9
Brook lamprey	12.0	527	3.9 (9.6)	1.6
Salmon	11.2	492	26.5 (35.1)	13.1
Perch	10.1	441	4.1 (7.5)	1.7

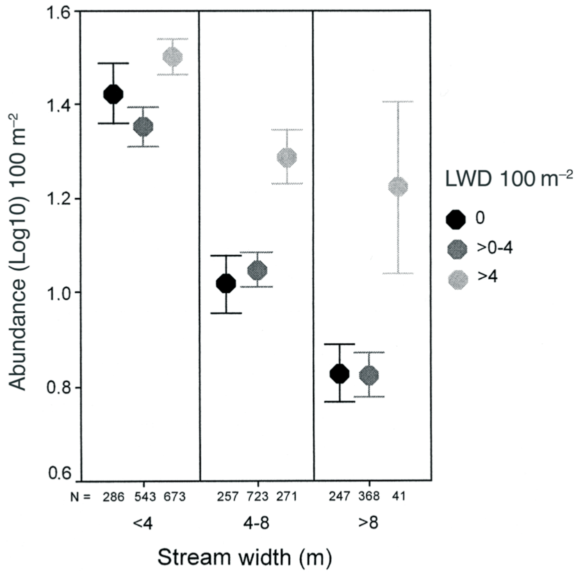

Fig. 2. Abundance ($\log_{10}$ no. 100 m^{-2}) of brown trout versus stream width class and LWD-class. Bars indicate 95% confidence intervals.

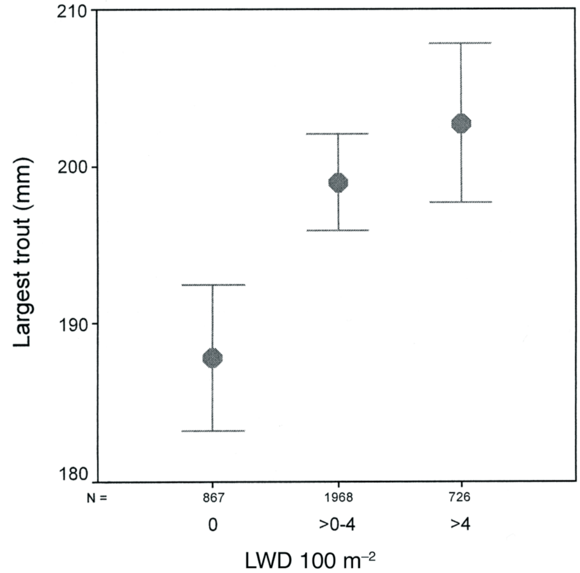

Fig. 4. Length of largest caught brown trout (mm) at each fishing occasion versus the amount of LWD present (expressed as no. 100 m^{-2}). Bars indicate 95% confidence intervals.

(SD=68 mm) at sites without LWD (n=861) and 200 mm (SD=69 mm) at sites with LWD (n=2661). This difference was significant even after the effects of latitude, maximum depth and $\log_{10}$-density of trout >0+ were compensated for (Ancova with three covariates and LWD-class, presence/absence, as fixed factor, $p<0.001$ model, $p=0.046$ LWD, $r^2=0.14$). There was no significant difference between sites with low quantity of LWD as opposed to sites with more LWD (Fig. 4).

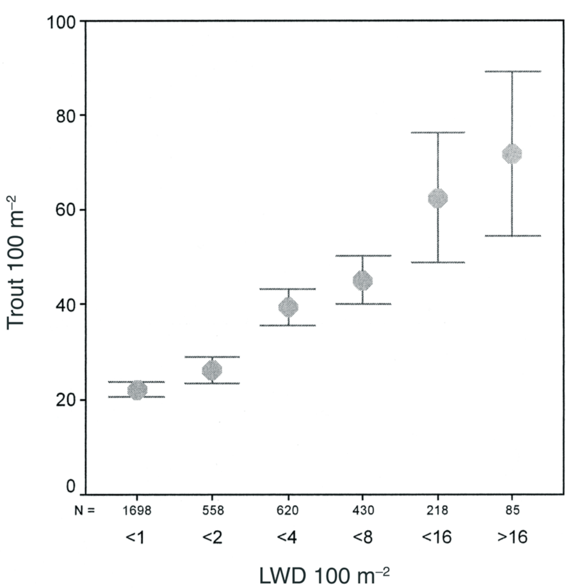

Fig. 3. Abundance (no. 100 m^{-2}) of brown trout versus quantity of LWD. Bars indicate 95% confidence intervals.

Size of trout of the age class 0+ is an indirect measure of growth during the first season, but the size is heavily dependent on sampling date and comparisons must be done with this in consideration e.g., by using Julian date (1–366) as covariate. The largest 0+ averaged 72.7 mm with no LWD, 70.9 mm when LWD >0–4, and 71.1 mm when LWD >4 pieces 100 m^{-2}. This decrease in underyearling size was significant (Ancova with LWD-class as fixed factor and latitude, altitude, Julian date and $\log_{10}$ abundance of 0+ as significant covariates, $p<0.001$ model, $p<0.001$ LWD, $r^2=0.474$). When the effects of the covariates were taken into account, new averages for the three LWD-classes could be calculated: 73.3, 71.5 and 68.7 mm, respectively. This means that average size of the largest underyearling was 6% lower when comparing sites without LWD to sites with >4 pieces of LWD.

Discussion

Trout and dead wood

Brown trout was the most common fish species in the investigated forest streams. Whereas occurrence increased with stream width, abundance was highest in the smallest streams. The occurrence and size of the largest trout were higher at sites with LWD present than at sites without LWD. This indicates that LWD creates a suitable environment for a trout, probably by providing a station sheltered both from predators and water current (Tschaplinski and Hartman 1983, Fausch and Northcote 1992), and possibly by creating pools, a habitat that generally has larger trout than other habitat types (Heggenes 1988). Increased size, occurrence and abundance of trout with the amount of LWD indicate that suitable sites/stations (for foraging and refuge) may be limiting factors for trout (Bachman 1984). It should be noted that the abundance generally increased three times from sites without LWD to sites with >8 LWD pieces 100 m^{-2}. That the abundance of trout increased up to quantities of >8 pieces of LWD 100 m^{-2}, and that such levels of abundance occurred only at 6% of the sampling sites, indicate that the production can be limited by LWD at the landscape scale.

The effect of LWD on trout was particularly evident in larger streams (Fig. 2). In narrower streams the stream bank, submerged roots and probably the shading per se create suitable microhabitat. It is also plausible that the shelter against water currents created by LWD is more important in larger streams that naturally have higher water velocities. The recorded decline in underyearling size, and indirectly growth, can be an effect of increased trout populations along with increased quantity of LWD. This would indicate a density-dependent effect on growth at higher densities, which has been shown previously for brown trout in small streams (Nordwall et al. 2001).

It is known that the quantity (Andrus et al. 1988, Valett et al. 2002) and diameter (Rot et al. 2000) of LWD increase with forest age. Hence, the introduction of forestry to naturally dynamic landscapes normally decreases the amount of LWD supplied to the streams (Valett et al. 2002). Half of the amount of LWD is lost from forest streams within 20 yr, and virtually all of the wood will have disappeared within 50 yr (Hyatt and Naiman 2001). Hence, salmonid production may be substantially lowered 20–60 yr after a clear-cut (Connolly and Hall 1999). In Sweden, >95% of the forested area is managed, i.e., subjected to clearcutting, for several decades without sound watershed management principles. There is a lack of holistic and multidisciplinary perspectives in management of watersheds that have been drained and are dominated by conifer re-forestation. There are also obvious gaps in the functionality of managed landscapes where processes like fire and flooding do not longer continuously maintain old forest and dead wood (Lazdinis and Angelstam in press). Despite the fact that several recent studies have clearly declared that protection of riparian zones is of essential importance to fish in rivers and streams, the information has rarely been implemented. As a consequence, riparian forests have been harvested and the amount of LWD in the streams has been impoverished. In the present study the median quantity of LWD 100 m^{-2} was 1. This result can be compared to North American studies on streams with pristine conditions where the measured density of LWD m^{-2} varied between 0.3 and 17 (Bilby and Ward 1989, Murphy and Koski 1989, Fausch and Northcote 1992, Ralph et al. 1994, Flebbe and Dolloff 1995).

This study indicates that a substantial loss of salmonid production may be a result of diminished amount of LWD in managed forests compared with naturally dynamic riparian landscapes. In some restoration programmes LWD has been artificially added to create a more diverse aquatic habitat. Larson et al. (2001) studied such projects and found that the effect of a single effort only affected stream physical habitat in 2–10 yr and that the effects on biota were small. Obviously, a naturally dynamic riparian landscape with a mixture of young and old trees, which continue providing LWD to the streams, cannot be replaced by artificial substitutes. Hence, it is essential to study LWD in forest streams to quantify the natural amount of LWD that should be present.

Towards aquatic gap analysis

Habitat loss is known as the major factor affecting directly or indirectly the global decline of biodiversity (Heywood 1995, Wilcove et al. 1998). Hence, with a biodiversity conservation perspective, the evaluation of hypotheses claiming species-specific "extinction thresholds" defined as the minimum amount of habitat required for the persistence of species in the landscape is an urgent task (e.g. Lande 1987, Andrén 1994, Ehrlich 1995, Fahrig 1997, 2001, Sih et al. 2000, Angelstam et al. 2004). Apparently, human-driven landscape changes have resulted in the trespassing of such critical levels of habitat loss, e.g. in the form of LWD or the habitat features created by LWD, for many species (e.g. Harmon et al. 1986). This has then caused the extirpation of species. Consequently, the question "how much habitat is enough" has recently received a lot of attention from policy makers and managers dealing with biodiversity issues (e.g. Higman et al. 1999, Duinker 2001). However, for aquatic ecosystems there is no tradition of systematic analyses for conservation planning and restoration management in Scandinavia.

Gap analysis is a tool for strategic assessment of the extent to which environmental policies succeed in maintaining biodiversity by protection, management and restoration of habitats (Scott et al. 1993, 1996). Originally developed in the USA, gap analyses have been used in terrestrial systems to increase society's awareness about conservation needs and to guide the practical implementation of such policies. The rationale for focusing on habitat (i.e. structural elements of biodiversity) is that it serves as a proxy for the maintenance of viable populations of species, vital ecosystem processes and resilience to external disturbance (e.g. Karr 2000).

Originally gap analyses focused on representation i.e., that the different types of conservation areas should reflect the natural composition of different ecosystems (see Margules and Pressey 2000). Angelstam and Andersson (2001) developed the idea further by combining measurements of the habitat area with information about thresholds for the amount and quality of habitats needed to maintain viable populations within an ecoregion. This approach has also been applied recently in Estonia (Lõhmus et al. 2004).

There is a growing insight that there are complex interactions between the terrestrial and aquatic systems, which require transdisciplinary landscape approaches such as aquatic gap analysis (Rabeni and Sowa 2002, Schneider et al. 2002). For example, the multimetric index of biological integrity (IBI) was developed as an offshoot of basic research in aquatic ecology (Karr 2000). Effective indices require indicators that are either theoretically or empirically flawed (see Karr and Chu 1999 for a review). They contain elements of biodiversity that are sensitive to a broad range of anthropogenic disturbances such as sedimentation, organic enrichment, toxic chemicals and flow alteration. Common metrics are species composition and habitat structure.

However, we do not know what the quantities of LWD of dead wood are in naturally dynamic benchmark ecosystems, nor the extent to which brown trout indicates other elements of biodiversity in small rivers. Three kinds of studies are therefore needed. First, brown trout should be sampled in a wider range of LWD. Second, the LWD index should be calibrated to quantitative data in riparian zones that can be communicated to forest managers. Third, the degree to which trout presence indicates diversity in other elements of biodiversity (Lambeck 1997, Roberge and Angelstam 2004), should be studied.

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