





­Running head:

TITLE

The relative importance of direct and indirect effects of large scale and local factors for stream fish population

Direct and indirect effects of large and small-scale drivers of fish abundance in streams

Dead wood mediates effects of large and small-scale factors on fish abundances in stream ecosystems

Manuscript type: Article

**ABSTRACT**

Identifying drivers of fish abundance in running waters is challenged by high variation in physical conditions at both large and local spatial scales. Several fish species perform migrations upstream and downstream, covering longitudinal gradients in climatic and geographic factors. Moreover, streams typically encompass highly diverse adjacent habitats, where environmental conditions, such as water velocity, depth, and substrate, vary within short spatial ranges. Among the local-scale factors affecting fish abundance, the occurrence of woody debris has been reported to boost salmonid fish population growth. However, what species benefit from woody debris, to what extent relative to other biotic and abiotic drivers, and what factors influence woody debris local quantity is not clear yet, which limits our ability to use woody debris as an effective restoration measure.

We analyzed time series data collected between 1993 and 2016 from 3653 rivers (total of ca 7000 sampling sites) all over Sweden to investigate 1) the relative importance of large-scale and local factors for the abundance of three key freshwater fish species: salmon (*Salmon salar*), brown trout (*S. trutta*), and sculpin fish (*Cottus* spp.), 2) whether local abundance of woody debris has beneficial effects on these three species, and 3) the drivers of woody debris persistence.

We found that large-scale factors such as annual mean air temperature and altitude mainly explained *Cottus* abundance (negative effects), while local stream width was the strongest predictor of trout and salmon abundance, with negative and positive effects, respectively. Trout abundance also decreased with local stream depth and abundance of burbot, a predatory species, while it increased with mean air temperature. Woody debris appeared to benefit trout, but not salmon or *Cottus* spp. abundance. The quantity of woody debris strongly decreased with stream width, but also depended, albeit to a lesser extent, on stream bed slope, forest age and cover, altitude, and mean air temperature. Our study suggests that the weight of large- and local-scale factors on fish abundances in streams varies strongly with species, and that effectiveness of woody debris as a restoration measure depends on both the targeted species and local environmental conditions.

**Keywords**:

**INTRODUCTION**

Both economically and non-economically valuable fish population provides a range of ecosystem services for human societies (Holmlund and Hammer 1999). Fish populations are however undergoing increasing pressures (e.g. overfishing, habitat loss, climate change REF) in both marine and freshwater ecosystems, and is therefore crucial to understand drivers of abundance and distribution to aid management and conservation.

~~Theory and empirical studies show that distributions of fish among other species are generally determined by abiotic factors at regional scales (check Jenkins and Ricklefs 2011).~~

It is commonly accepted that large-scale processes/ processes acting on larger spatial and temporal scales structure species assemblages/determine the coarse distribution of species by selecting/filtering the pool of potential available species/by determining the potential range that any given species can occupy (Tonn et al. 1990, Ricklefs 1987, Moran-Lopez 2012). On the other hand, behavioral, morphological, and physiological adaptations to local conditions, as well as biotic interactions (competition and predation), have a strong influence on where and when a species will be found (Grossman et al. 1998 in Jackson et al 2001, Jackson et al 2001, Tonn 1990). A number of studies has addressed fine-scale habitat use, often in relation to competition and predation (e.g. check Gorman & Karr, 1978; Schlosser 1982 in Moran-Lopez and find recent), while others have focused on large-scale drivers of distribution across systems./major abiotic constraints at large-scales (e.g. Magalhaes et al., 2002).So far, however a unified approach for understanding the relative importance of large and small scale drivers has rarely been implemented due to/ been prevented by the availability of resources to data collection, as well as the questions considered (Jackson et al. 2001). An integrated framework would be especially helpful for management purposes, as habitat restoration measures typically focus on the modification of local conditions (e.g other + removal of predators or competitors ….) to the benefit of the targeted species but have no power on large-scale drivers. Moreover, the effectiveness of such restoration measures may be conditional on the specific abiotic and biotic context considered. It is therefore important, for both our ecological understanding and management purposes, to evaluate together the relative weight of large-scale, small-scale and biotic factors in driving species distribution, and to assess potential context-dependent (interactive) effects.

The assessment of the relative importance/The identification of relevant drivers of fish abundance in running waters is further challenged by broad variation in environmental conditions at multiple spatial and temporal scales /at both large and local spatial scales (Jackson et al. 2001, Cooper et al. 1998 find more recent). Rivers typically form vast interconnected networks that include strong longitudinal gradients of climatic and geographic factors, ~~and many fish species migrate long distances upstream and downstream~~. Maybe example of how large scale factors influence one rather than another spp. On the other hand, streams offer a multitude of different habitats, where local conditions such as depth, water velocity, and substrate composition can vary widely within shoirt spatial ranges (within few meters) and over time (due to fluctuations in stream flow) (Cooper et al. 1998, Grossman and Freeman 1987 find more recent). Maybe example of small scale factors Among the local-scale factors affecting fish abundance, the occurrence of woody debris is thought to benefit fish population growth (REF). more details on why, what spp.. However, what species benefit from woody debris and to what extent relative to other biotic and abiotic drivers is not clear yet. Furthermore, we know little about the factors driving woody debris abundances and persistence, which limits our ability to use woody debris as an effective restoration measure.

In the current study we analyzed time series data from 3653 rivers (total of ca 7000 sampling sites) across Sweden to investigate 1) the relative importance of large-scale and local factors for the abundance of three key freshwater fish species: salmon (*Salmon salar*), brown trout (*S. trutta*), and sculpin fish (*Cottus* spp.). Specifically, we asked 2) whether local abundance of woody debris had beneficial effects on these three species, and 3) what drivers determined woody debris persistence. We used path analyses (REF), which allows not only to evaluate the relative strength of multiple causal links/drivers within the same framework, but also to assess indirect effects, hence the significance of woody debris as mediator factor for fish abundances.

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This has important implications from a management perspective.

Sentences

Understanding drivers of fish abundance in running water is pivotal/essential for conservation and effective restoration.

Understanding drivers of fish abundance in running water is challenged by high spatial and temporal variation in physical conditions at both large and local scales.

However Moreover, streams also/typically encompass high spatial and temporal variation in local conditions, such as water speed, depth, slope, substrate type./Furthermore, physical conditions in streams can vary strongly on short spatial and temporal ranges, thus offering a variety of habitats/resulting in highly diversified habitats on short ranges.

Third/finally, biotic pressures such as competition and predation may further constrain the occurrence

Such high large and small scale spatial variability together with seasonal variations, long term dynamics and the effects of predators and competitors /High large and small scale variation in physical conditions, together with biotic drivers of fish distribution such as competition and predation, challenge our understanding of the relative importance of large- vs local-scale drivers of fish abundance in streams

**METHODS**

From trigal: Fish and environmental data were drawn from the Swedish Electrofishing Register (SERS), a database containing more than 56500 records from 17500 sites sampled across Sweden from 1951 onwards. For this study we selected a subset of 2005 lowland sites sampled at least once between 2000 and 2011. The study sites were located at altitudes lower than 200 m a.s.l (see Fig. 1). This boarder coincides roughly with the Swedish highest coastline, which acts as a natural barrier and plays a role in limiting the dispersal of lowland fish species into streams at higher altitudes (Ekman, 1922).Weselected sampling sites with a wetted width less than 10 m, due to the reduced effectiveness of electrofishing by wading in wide streams (Kennedy and Strange, 1981). Water temperature at the time of sampling ranged from 5 °C to 27 °C. The surrounding landscape consisted of forest, with coniferous species dominating, and agricultural lands, particularly in southern Sweden. Other environmental variables are described in Table 1

From egerman 2000: Electrofishing data were compiled from the Swed- ish Electrofishing RegiSter (SERS), which com- prises approximately 16,000 electrofishing oc- casions at 7500 different localities. Only localities in the northern part of Sweden, within or north of the River Dala ¨lven catchment (approx. north of 60æN), were included (nΩ3146), since this is the main area where grayling and brown trout coexist in Sweden. Most data stem from electrofishing sur- veys made in August or September, i.e. when underyearlings of these species can be reliably cap- tured.Electrofishing was generally carried out using DC-equipment from LUGAB or BIOWAVE, Sweden. The abundance of fish was determined by successive-removal fishing according to Bohlin (1984). At localities where successive removal was not performed the total abundance of fish was esti- mated on the basis of average catch probabilities for the respective species and age groups (Sers & Degerman 1992). The fish were measured to the nearest mm total

length, but were not weighed or sexed. Classifi- cation of brown trout and grayling into the age groups underyearling (0π) and older fish was based on length frequencies. In cases where age de- terminations were difficult, otoliths were used, or the fish were omitted. For each locality the geographical location (lati-tude, longitude and altitude), stream width, aver- age depth, maximum depth, and air and water temperatures were recorded. The bottom sub- stratum was classified into five categories (1–5; fine (∞0.0002 m), sand (0.0002–0.002 m), gravel (0.002–0.02 m), stones (0.02–0.2 m), boulders (±0.2 m)), with coarser particles being given a higher value. The sampling sites were classified based on their average surface-water velocity into three categories (1–3), i.e. slow stretches (∞0.2 m ¡ sª1), intermediate stretches (0.2–0.7 m ¡ sª1) and rapids (±0.7 m ¡ sª1). In addition, the dis- tances from each sampling locality to lakes up- stream and downstream were recorded. Catchment areas were classified into four size categories: ∞10 km2, ∞100 km2, ∞1000 km2 and ±1000 km2. The proportion of lakes of the upstream catchment was classified into four categories: ∞1%, 1–4.9%, 5– 10%, ±10%.

From ohlund: Swedish electrofishing register (SERS) In SERS, a database containing more than 12 000 studied sites (32 448 fishing occasions) in Swedish streams, standard- ized electrofishing data are provided by various organizations and authorities. Population densities of different species are calculated according to Bohlin et al. (1989) when electro- fishing is made in successive removals. If only one removal is made, densities are calculated from the average catch effi- ciency of the given species and age class (Degerman and Sers 1999). At the fishing occasion, water temperature is measured at a midstream depth of 0.3 m. Altitude (m a.s.l.) and latitude are measured from maps to the nearest 1 m and 10 m, re- spectively, for each locality. Stream width, average and maximum depth, dominating substrate, and water velocity are measured in the field. The proportion of lakes in the up- stream watershed is classified into four area classes: <1%, 1%–5%, 5.1%–10%, >10%. The size of the upstream water- shed was also classified from maps: <10 km2, 10–100 km2, >100 km2. The date of fishing was expressed as Julian date (ranging from 1 to 366). The entire database was used for one comparison of the stream size related relative occur- rence of brown trout and brook trout.

For comparisons of densities, a subset of data was se-lected. In SERS, brook trout were present on 520 localities. From these sites, 500 were randomly selected. For each of these 500 localities, the nearest brown trout locality without brook trout was chosen as reference. Each brown trout local- ity was always in the same watershed size class (<10, 10– 100, >100 km2) and basin as the corresponding brook trout locality and was not allowed to deviate by more than 50 m in altitude from it. Localities used in the analysis ranged from the counties Skåne to Västerbotten (hence distributed over roughly two-thirds of Sweden’s surface area) and were located in the altitudinal range of 1–648 m a.s.l. When data from several fishing occasions were available, the latest oc- casion was chosen. Brown trout localities did not deviate in altitude from brook trout localities (t test, t = 0.073, p > 0.05; mean values of 305 and 300 m a.s.l. for brown and brook trout, respectively). Given the methodology of select- ing reference localities, there was no difference in geograph- ical average position (longitude and latitude, i.e., x and y coordinates) or watershed size. In analyses, data were pooled in four classes: brook trout present (n = 500), allo-patric

**RESULTS**

Both large- and local-scale factors affected the abundances of the study fish populations, but their relative importance varied with species (maybe redundant, remove?). Large-scale factors such as year air temperature and altitude mainly explained Cottus abundance (negative effects), while local stream width was the strongest predictor of trout and salmon abundance, showing negative and positive effects respectively. Trout abundance also decreased with stream depth and abundance of the predator turbot, and increased with year air temperature, while salmon abundance decreased with altitude.

LWD appeared to benefit trout but not salmon and Cottus populations. The abundance of LWD strongly decreased with stream width, but also depended, albeit to a less extent, on stream bed slope, forest age and cover, altitude and average air temperature.

**DISCUSSION**

By looking at data it seems like Cottus distribution is mainly determined by large scale factors, while salmonids respond promptly to variation in local conditions. As large-scale drivers typically define the fundamental niche of species, while small-scale factors define the applied niche of species, our results suggest that salmonids may undergo higher competition/predation pressure than Cottus.

Wootton 2017: wood debris may decrease omnivore interactions therefore increase stability of communities.(These predictions are important for effective freshwater management because actions which decrease the strength of omnivorous interactions, such as main- taining habitat refuges for consumers (e.g. woody debris and aquatic plants), may be essential for sustaining biodiversity.)

hierarchical screening provided by Smith and Powell (1971) . also Tonn 1990: fish assemblages are structured by a series of filetrs. But it does not talk about their relative importance

look at Jackson et al 2001

ACKNOWLEDGEMENTS

REFERENCE LIST

TABLES

Table 1. Path coefficients (single-headed arrow) and correlated errors (double-headed arrows) from the best-supported structural equation model (Figure 5). The last column shows the link function for each component model (see Materials and Methods for details).

FIGURES