Will Atlantic salmon (*Salmo salar* L.) colonize restored tributaries in the river Vindelälven, northern Sweden?

Erik Mellgren
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Kommer Atlantlax (*Salmo salar* L.) att kunna kolonisera restaurerade biflöden i Vindelälven, norra Sverige?

Erik Mellgren

Keywords: Atlantic salmon, *Salmo salar*, parr, juveniles, spawning, habitat, Vindelälven, floatway restorations, colonization, tributaries

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Abstract
The Vindelälven River and its tributaries have been severely affected by log floating activities during the past two centuries. During the last decades intense efforts to restore the habitat have been implemented. At present the spawning stock of Atlantic salmon in river Vindelälven is increasing, and as the population grows, fish start to seek new habitats suitable for spawning. Such habitats may be tributaries. This study evaluates if the restorations in the tributaries produce the necessary prerequisites for salmon spawning and nursing. Nine known salmon parr nursing sites in the main stem were sampled with regards to depth, water velocity and substrate composition, and then compared to the habitat characteristics of ten restored nursing sites in the tributaries. In general, tributary nursing sites were very similar to nursing sites in the river (> 65 % similar), both with regards to depth, velocity and the composition of substrate. Radio tagged adult salmon were used to locate twelve spawning sites in the main stem. Measurements of depth, velocity and substrate at these locations were taken on the spawning sites and used as a reference material to which habitat data for 39 restored tributary spawning sites were compared. The average river spawning site was significantly deeper than the tributary spawning beds and was composed of in average courser substrates. Water velocities were similar between river and tributary sites. The study concludes that salmon can utilize the tributaries as nursing grounds, but it remains unclear whether spawning prerequisites are fulfilled.

Introduction
Fish stocks all over the world, and in all waters, are threatened due to human impact (Karlsson & Karlström 1994; Jackson et al. 2001; Myers & Worm 2003). The Baltic Sea is no exception as several species of fish have been severely affected and reduced in numbers and distribution range due to overexploitation and habitat degradation (Karlsson & Karlström 1994; Vallin et al. 1999; Casini et al. 2008). Today, species as Atlantic salmon show signs of spatial recovery, and are again beginning to expand their distribution ranges in the Baltic Sea (Cardinale & Svedäng 2011; McKinnell & Karlström 1999; ICES 2012).

The wild populations of Atlantic salmon in the Baltic Sea have drastically declined the last 60 years (Mckinnell & Karlström 1999). Originally 44 salmon stocks were found in the rivers spilling out in the Gulf of Bothnia, today only 12 wild stocks remains (Karlsson & Karlström 1994). Hydropower, pollution, mixed-stock fishing and log-floating activities have had an extremely negative effect on Baltic salmon stocks since the 19th century (Karlsson & Karlström 1994; Eriksson & Eriksson 1993; Nilsson et al. 2005; Romakkaniemi et al. 2003).

To counteract these negative effects, many different mitigation measures to improve the living conditions for many Baltic salmon stocks have been implemented the last couple of decades, e.g., construction of fish passages, commercial fishing regulations ((EC No 812/2004), shifting from pelagic to coastal fisheries to decrease the problems associated with mixed-stock fishing (Rydgren 2011), and habitat restoration of rivers and streams (Nilsson et al. 2005; Näslund 1989). Signs of recovery can now be seen in some of the Baltic populations, especially in the larger northern mountain rivers (ICES 2012). Increasing salmon populations
may result in individuals searching for new spawning sites in areas yet not occupied by salmon; e.g. expansion into tributaries.

In the nineteenth century utilization of forests for timber became profitable (Törnlund 2002) and most Swedish rivers and tributaries were used as float ways for timber to coastal industries (Törnlund & Östlund 2002; Näslund 1989). In order to facilitate the transport of timber the watercourses were channelized (Palm 2007; Nilsson 2007). Big boulders and large woody debris were removed to avoid log jams and stone piers were constructed to cut off side channels and eddies to create one single mainstream (Törnlund 2002; Nilsson et al. 2005). Float way alterations were done in about 30,000 km of Swedish watercourses (Törnlund 2006; Palm 2007).

Log floating has caused numerous problems for salmonids inhabiting Swedish watercourses. Removal of stones and larger holding structures led to reduction in salmonid spawning habitat (Talbot & Lapointe 2002; Palm 2007). Channelization and homogenization of habitats reduced nursing areas (Palm 2007), and number of territories for juvenile salmon parr decreased. Smaller streams lost their ability to retain allochtonous material (Lepori et al. 2005) resulting in ecological impact throughout the food web, such as lower overall production (Wallace et al. 1997). Splash dam constructions became migration hinders for salmonids migrating to spawn or migrating to suitable winter habitat (Nilsson 2007). A number of restoration measures have been implemented to restore damages made by floating, and to create habitats similar to the pristine conditions (Nilsson et al. 2005). Suitable spawning habitats are of vital importance to all salmon stocks. Jonsson et al. (2003) argued that straying occurs more often when the spawning opportunities in the home river is degraded. It implies that when salmon stocks increase, prime spawning habitat will become saturated with fish, forcing individuals to seek out new habitat suitable for spawning and nursing. In Sweden, salmon spawning are generally thought to occur in the main stem of rivers (Östergren 2003). Juveniles of Atlantic salmon are also generally found in the main stem of rivers, often along the littoral zone or in small side-branches (Swedish Electrofishing Register – SERS). However, such generalization of salmon spawning and nursing habitats is based on very low population abundances, with no effective density dependent mechanism in place to push individuals to occupy new habitats. In recent years however, salmon parr have also been observed in tributaries in rivers where populations of salmon are increasing rapidly (SERS). However, little is known about tributary suitability with regards to salmon. In connection with the possibility that salmon may begin utilizing tributaries, it is important to better understand their potential as areas for salmon spawning and as juvenile nursing areas.

The aim of this study was to investigate whether the restoration efforts in the tributaries produce the required prerequisites for salmon to utilize the tributaries for spawning and as nursing habitat. Evaluation of tributary habitat quality is based on comparing the habitat characteristics of restored nursing and spawning sites in the tributaries to the habitat characteristics of known salmon nursery and spawning sites in the main stem. The study focus on the habitat variables depth, water velocity and substrate size. Habitat similarity between tributaries and main stem sites would indicate that the tributaries are suitable to salmon. My
study also evaluates the use of general suitability indexes (Mäki-Petäys et al. 2002) to estimate the quality of salmon parr habitat.

Materials and methods

Study site
The study took place in the Nature-2000 catchment of river Vindelälven, focusing on habitats in both the main stem and in tributaries. River Vindelälven has its origin in the Scandinavian mountains and runs in a southeasterly direction for approximately 400 km before joining river Umeälven about 42 km upstream the outlet in the Bothnian Bay (63°50’N, 20°05’E) (Figure 1). Vindelälven follows a snow-dominated flow regime. Average annual discharge is 180 m$^3$•s$^{-1}$ and minimum winter discharge of 40 m$^3$•s$^{-1}$. In June the flow reach its peak at ca. 1,000 m$^3$•s$^{-1}$ during snowmelt. Ice covers the river from November to April. The fish fauna is predominated by Atlantic salmon, brown trout, northern pike (Esox lucius), Eurasian minnow (Phoxinus phoxinus), burbot (Lota lota), Eurasian perch (Perca fluviatilis), European grayling (Thymallus thymallus), and European sculpin (Cottus gobio) (SERS). The riparian surroundings consist of managed boreal forest mainly composed of Scots pine (Pinus sylvestris) and Norway spruce (Picea abies).

Since 1958, river Vindelälven is affected by hydropower. Approximately 10 km downstream the river Vindelälven’s outlet in the river Umeälven is Stornorrfors hydropower plant located (Figure 1). A fish passage was constructed when the hydropower plant was built 1958 to allow fish to migrate upstream, and recently a new passage has been constructed (Vattenfall 2008). River Vindelälven has suffered severely from floating activities in the past (Törnlund & Östlund 2002; Törnlund 2006; Palm 2007). Big boulders and LWD were removed and stone piers were constructed in the river and its tributaries with huge biological impacts (Nilsson et al. 2005; Lepori et al. 2005; Wallace et al. 1997; Nilsson 2007; Palm 2007). In River Vindelälven salmon is only known to spawn in the main stem and primarily the spawning occur on a 35 km reach located in the center of its course ca. 230 km upstream the coast, however spawning also occurs scattered in other parts of the river (Östergren 2003). In 2013, ca. 10,000 salmon passed upstream for spawning. Electrofishing monitoring programs have been conducted in the main stem and in the tributaries since 1990. Therefore the development of salmon parr densities is well known.

Field survey – Nursery sites
Habitat data from nine nursery sites (Figure 1) in the main stem was collected in the end of September. At each site ten transects with five sample plots each were inventoried. Transects were laid out perpendicular to the shoreline and were spread out as evenly as possible across the site. The size of the sites differed due to natural conditions, i.e water depth and velocity. The data collected at each sample plot were: depth, surface velocity, half depth velocity, near bed velocity and diameter of the dominant substrate. The depth was measured using a ruler and the velocity was measured with a flow meter (C2, A. Ott, Kempten, Germany). Each velocity value in the data set is a mean value of ten measurements with a standard error of maximum 0.1. The dominant substrate size was estimated by eye using an aquascope. Salmon parr densities in these nine nursery sites were obtained from the Swedish electro fishing
Field survey - Spawning sites
Habitat data from twelve spawning sites in the main stem was collected in late October 2012. The spawning sites were located using radio-telemetry tagged salmon. The salmon were radio tagged during the summer just downstream the fishway in Norrfors (lower Umeälven) (Figure 1). During the spawning period radio tagged salmon were located within approximately 10X10 meter square. Habitat data (depth, water velocity and substrate) at the sites were collected from boat. Water velocity was measured throughout the water column in 10 cm cells using an Acoustic Doppler Current Profiler (ADCP). The size of substrate was measured using a submerged IR-camera operated from the boat. Substrates were divided in frequency distributions of the sample area and according to a modified Wentworth scale (1, < 32 mm; 2, 32,1 – 64 mm; 3, 64,1 – 128; 4, 128,1 – 256 mm; 5, 256,1 – 512 mm; 6, 256,1 – 1024 mm; 7, bedrock). Habitat data, collected in the tributaries according to a slightly different methodology, was obtained from www.vindelriverlife.se. In the tributaries, the water velocity was measured at five different relative depths per sample and the substrates were inventoried by measuring 30 random stones per restored spawning bed.
Fig 1 River Vindelälven with tributaries involved in the study. Radio-tagging location for salmon at the lower part of Umeälven (Norrfors fish ladder) shown in the figure.

Analysis

Habitat characterization and comparison

To characterize different habitat types for both potential spawning and growth areas for juveniles in this study, the variables depth, velocity and substrate were used. These habitat variables are widely used to describe fish habitat (e.g Mäki-Petäys et al. 2002; Sheppard & Johnsson 1985; Aadland 1993). In this study three methods were applied to compare these habitat variables in the main stem and in the tributaries, 1. Mäki-Petäys et al. (2002) suitability indexes, 2. Coefficients of variance, 3. Czekanowski overlap index.

1. Mäki-Petäys et al. (2002) created parr suitability indexes for these three habitat variables to predict parr densities. Each variable separately gives relatively little information about the habitat. Therefore Mäki-Petäys et al. (2002) created a joint suitability, which is the geometric mean of the suitability indexes for the three habitat variables. The suitability indexes categorize how suitable the living conditions are in the parr habitat giving each nursery site a relative value between 0 and 1, where 0 is unusable habitat and 1 is the optimal habitat. To
create these indexes Mäki-Petäys et al. (2002) compared parr densities with the availability of habitats, meaning that high parr densities in low abundant habitat indicate good habitat.

2. Coefficients of variance give a relative measure of the spread of the variable observations. As the coefficient of variance is expressed as percentage it is readily comparable between sites. In this study, the coefficient of variance is used as a measure of habitat heterogeneity.

3. To evaluate the similarity between tributaries and river sites, Czekanowski overlap index was used. The Czekanowski overlap index quantifies the area of intersection between two frequency distributions. In other words, how much the distribution of depths in the tributary sites overlapped with the river reference sites.

Nursery sites

To investigate whether Mäki-Petäys et al. (2002) suitability indexes could be used to predict salmon parr habitat in the main stem of river Vindelälven, the suitability indexes were correlated to the parr densities. The nursery sites in the river were ranked based on their suitability score, as well as their parr 0+ densities. The rank order of the suitability score was then correlated to the rank order of parr 0+ density, using Spearman rank correlation coefficient. The Spearman rank correlation coefficient calculates how well two different rankings correlate.

Variance coefficients for depth, velocity and substrate habitat variables were calculated for each tributary site, as well as for the river reference. A general measure of habitat variability was achieved by calculating the geometric mean of the variance coefficients for all three variables (depth, velocity and substrate). I examined if high coefficients of variance (i.e habitat heterogeneity) were correlated with high parr density by ranking the nursery sites in the river based on their variance coefficient and then correlated these measures to parr densities, using the Spearman rank correlation coefficient.

Czekanowski overlap index was used to evaluate the habitat similarity between the restored nursery sites in the tributaries and the observed salmon nursery sites in the river. The Czekanowski overlap index calculates the area of intersection between two frequency distributions, i.e., how similar two frequency distributions are. The Czekanowski overlap index was done by dividing the data into frequency distributions. Substrate data was divided according to the same modified Wentworth scale that were used in the restoration sites habitat inventory with 6 categories (Cat (category) 1 <2,1 mm; Cat 2, 2,1 – 64 mm; Cat 3, 64,1 – 256 mm; Cat 4, > 256 mm; Cat 5, bedrock; Cat 6, organic material). The depths were divided in 10 cm intervals and the velocities in 10 cm/s intervals, following the recommendations of Mäki-Petäys et al. (2002). The chosen depth and velocity intervals were based on the assumption that parr can distinguish and prefer one category over another. All sites in the river with salmon parr 0+ densities that exceeded 20 individuals per 100 m² were used as a reference (river reference). The river reference may be regarded as good habitat since 20 individuals per 100 m² are considered to be at least moderate densities (Palm pers. comm. 2013). Czekanowski overlap index was used to compare habitat between the river reference and each restored site in the tributaries.
Spawning sites
Velocities 30 cm from bottom were compared between the river reference and the restored
spawning beds in the tributaries. Due to technical problems, the ADCP-data did only contain
data down to a depth of 2 meters. Sites deeper than 2 meters therefore lacked data from the
river bed up to 2 meters from the surface. For these sites, velocities at 30 cm depth were
estimated assuming a power-function relationship between depth and velocities (i.e velocity =
a*depth^b, where a and b are constants derived from the data).

The sites in the main stem that were used for spawning by radio-tagged salmon were used as a
reference (river reference). Due to limited sample size, the Czekanowski overlap index is not
appropriate to describe habitat similarity for velocities and depths between restored spawning
beds in tributaries and spawning beds in the river reference. Instead, differences in depth and
velocities between tributaries and river reference were tested using welsh two-sample t-tests.

Czekanowski overlap index was used to describe the similarity between the river reference
and the restored spawning beds with regards to substrate composition. The substrates were
divided into a modified Wentworth scale (1, < 32mm; 2, 32,1 – 64 mm; 3, 64,1 – 128; 4,
128,1 – 256 mm; 5, 256,1 – 512 mm; 6, 512,1 – 1024 mm; 7, bedrock).

Results

Nursery sites

Suitability index (Mäki-Petäys et al. 2002)
Overall, the Mäki-Petäys et al. (2002) suitability indexes had a low correlation with parr
densities (Table 1). The indexes based on substrate had the highest correlation (r=0.25), whilst
index based on velocity had the lowest (r=0.03). Joint suitability indexes had a weak negative
correlation with densities, meaning that a higher suitability would indicate less parr.

Table 1 The ranking of nine nursery sites in river Vindelälven based on their suitability index (Mäki-
Petäys et al. 2002) for depth, velocity (half-depth) and substrate, as well as their densities of parr.
Spearman rank correlation index was used to correlate the rank order between par densities and
suitability index

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<tr>
<th>Parr 0+ density rank</th>
<th>Substrate suitability rank</th>
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Spearman rank correlation (r) - index

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Spearman rank correlation (r) - index

0.25 0.12 0.03 -0.07
**Variance of coefficient**

The mean of the variance coefficient for depth, substrate and velocity had a strong positive correlation with parr densities ($r=0.88$), indicating that a variable habitat had more salmon parr. Compared to depth and velocity, the variation in substrate had the strongest correlation to densities ($r=0.77$), meaning that high heterogeneity in substrate composition (with regards to size) will yield more salmon parr. Variation in velocities close to the bottom had a negative correlation with parr densities ($r=-0.45$), indicating that a site with homogeneous bottom velocities will be suitable to hold salmon parr. Variation in surface and half-depth velocity had low to moderate correlation with parr densities ($r=0.15$ to $0.17$).

**Table 2** The ranking of nine nursery sites in river Vindelälven based on their coefficients of variance for depth, velocity (surface, half-depth and bottom) and substrate, as well as their densities of parr. Spearman rank correlation index was used to correlate the rank order between par densities and variance coefficients. *Geometric mean of substrate, depth and half depth velocity. **Substrate divided in a modified Wentworth scale with 6 categories.

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| Spearman rank correlation (r) - index | 0.45 | 0.15 | 0.17 | -0.45 | 0.77 | 0.88 |

**Czekanowski overlap index**

Similarity in depth, velocity and substrate were moderately high between tributary nursing sites and the river references. The habitat overlap between tributary sites and the river references for substrates ranged between 63.4% to 90.8% (mean overlap = 78.6%) depending on what tributary site that was compared. For depth the overlap ranged between 53.8% to 79.2% (mean = 68.6%) and for velocity 62.4% to 83.6% (mean = 77.2%). Figure 2-4 gives illustrated examples of proportional overlap between a tributary site and river reference. See appendix for the remaining restoration sites.
Fig 2 An example of overlap in depth between a tributary nursing site (Falåströmbäcken) and the river reference. Depth is divided in frequency of occurrence – per interval. Dark blue bars, river reference (>20 parr/100m²); medium blue bars, tributary; light blue bars, overlap. This example shows the highest overlap found between the tributaries and the river reference.

Fig 3 An example of overlap in velocity between a tributary nursing site (Bjurbäcken) and the river reference. Velocity is divided in frequency of occurrence – per interval. Dark blue bars, river reference (>20 parr/100m²); medium blue bars, tributary; light blue bars, overlap. This example shows the highest overlap found between the tributaries and the river reference.
Fig 4 An example of overlap in substrate between a tributary nursing site (Mattjokkbäcken) and the river reference. Substrate is divided in frequency of occurrence – per category. Dark blue bars, river reference (>20 parr/100m²); medium blue bars, tributary; light blue bars, overlap. This example shows the highest overlap found between the tributaries and the river reference.

**Spawning sites**

*Depth and velocity*

There was a significant difference in mean depth between the river reference and the restored spawning beds ($t_{1,23} = -5.3$, $p<0.01$) (Fig 5), although no difference could be found regarding velocities ($p>0.05$) (Fig 6). 74% of the restored spawning beds velocities range is within the range of the river reference velocities (Fig 6).

Fig 5 Mean depth, as well as the shallowest and the deepest observation in the river reference (blue) and the tributary spawning beds (red). The river reference consists of all inventoried spawning sites in the main stem.

Fig 6 Mean velocity, as well as the slowest and the fastest observation in the river reference (blue) and the tributary spawning beds (red). The river reference consists of all inventoried spawning sites in the main stem.
**Substrate**
The average Czekanowski overlap index in substrate composition between the restored spawning beds in the EU-LIFE project and the river reference was 27.9% (min = 26.6%, max = 33.2%). An example of the overlap in substrate between a restored spawning bed and the river reference is presented in figure 7.

![Fig 7](image)

**Fig 7** An example of overlap in substrate between a tributary spawning site (Hjuksån) and the river reference. Substrate is divided in frequency of occurrence – per category. Dark blue bars, river reference (the inventoried spawning sites in the main stem); medium blue bars, tributary; light blue bars, overlap. This example shows the highest overlap found between the tributaries and the river reference.

**Discussion**

**Nursery sites**

*Mäki-Petäys et al. (2002) suitability indexes*

The low correlations between Mäki-Petäys *et al.* (2002) suitability indexes and parr densities indicate that the habitat preference of Vindelälven River salmon parr differ from that proposed by the suitability indexes. This suggest that the generality of Mäki-Petäys *et al.* (2002) salmon parr suitability index is low, and that river specific suitability indexes have to be used if one should be able to predict the quality of parr habitat. Guay *et al.* (2003) did not find a linear relationship between suitability index and parr densities, and reported that suitability indexes developed for a specific river could not predict parr densities in other rivers. For example, parr densities peaked at a joint suitability index of 0.7, i.e., lower than would be expected. Guay *et al.* (2003) argued that the difficulties to apply Mäki-Petäys *et al.* (2002) suitability indexes on high quality parr habitat (suitability index > 0.7) could be due to differences in substrate composition between rivers. This argument also follow Heggenes (1990) statement that habitat preference and habitat use is influenced by habitat availability. It implies that river Vindelälven might not have the structural habitat prerequisites to receive high correlation between suitability indexes and parr density. However, due to the limited sample size in this study, a closer evaluation of Mäki-Petäys *et al.* (2002) suitability indexes is recommended before excluding the possibility that the indexes are applicable as a guideline to evaluate suitability of parr habitat.
A methodological concern is that in the Mäki-Petäys et al. (2002) study, velocity suitability was measured at 0.6 * depth. In this study, Mäki-Petäys et al. (2002) velocity suitability values were applied at 0.5 * depth. However, it is a small source of error that probably is negligible.

Coefficients of variance
My data show that the geometric mean of variance coefficients for substrate, velocity and depth have moderate to high positive correlation with salmon parr densities in the river, concluding higher heterogeneity to yield more salmon parr. Tributary nursery sites had overall higher average heterogeneity regarding depth, velocity and substrate composition compared to the river reference, hence indicating that the tributaries should have a good ability to maintain salmon parr.

My data indicate that the coefficients of variance for habitat variables might be a good predictor of parr habitat quality, and further evaluation of the applicability of this measure is recommended. With increased heterogeneity, the parr obviously have access to more cover from predators and shelter from flow peaks. Habitat heterogeneity also tends to generate a more diverse fauna (Gue´gan et al. 1998; Gorman & Karr 1978), as more possible niches are available. Higher diversity also increases the overall productivity of the water, with positive effects for salmon parr.

Czekanowski overlap index
There was a substantial habitat overlap regarding depth, velocity and substrate composition between tributary nursing sites and river reference, indicating river and tributaries to have very similar abilities to contain salmon parr. The study therefore concludes that the necessary physical habitat characteristics to maintain salmon parr are fulfilled in the tributary restoration sites. These results are strengthened by electro fishing surveys in some of the tributaries of interest where salmon parr have been caught (Andreasson et al. 2005). Further, by comparing the habitat data from this study to preference data presented in other papers (Degraaf’s & Bain’s 1986; Heggenes 1990), the habitat in the restored sites seems to be suitable for salmon parr. Depth had the lowest overlap with the river reference, indicating that depth is the variable that limits parr densities in tributaries. However, there might be a methodological concern regarding that conclusion because the difficulties in performing electro fishing might vary between the main stem and the tributaries.

Several methodological considerations may be raised when using similarity indexes (like the Czekanowski index) to compare habitats. The habitat data needs to be in frequency distributions to perform Czekanowski overlap index. How large the area of intersections is between the diagrams depends on the size of the intervals in the frequency distributions. The intervals must be ecologically substantiated, i.e that parr can distinguish and prefer one category over another, to identify relevant differences. If the highest resolution possible would be used, the overlap would probably be quite low and also random, even if the habitats are similar. In this study, the intervals chosen for velocity and depth were based on the assumption that parr can distinguish between 10 cm/s velocity and 10 cm depth intervals. Those intervals are also consistent with earlier parr habitat studies (Mäki-Petäys et al. 2002;
Guay et al. 2003). Appropriate size of the intervals can be debated and it is important to understand that the Czekanowski overlap index is only a relative measure of similarity. In terms of the substrate, the chosen size categories had to be consistent with the modified Wentworth scale used in the tributary inventory to be comparable. However, a finer substrate scale would probably have more ecological relevance in this case. It seems like the Wentworth scale mainly is used in fish biology due to tradition and not based on its actual ecological relevance. The Wentworth scale was created in 1922 to obtain uniform geological definitions of different kinds of sized substrates (Wentworth 1922). Due to this initial geological use, the Wentworth scale often needs to be modified in different ways in research to be applicable on biology, and it can be discussed whether other scales would have more ecological relevance in fish biology.

The five sites in the main stem that had parr densities exceeding 20 individuals per 100 m² was used as reference sites to which the tributaries was compared using the overlap index. It can be discussed whether using the site with highest parr densities as a reference would be better than using average habitat data from the five sites. By using a broader reference spectrum one would capture a larger range of different quality habitats, thereby increasing the risk of including low quality habitats. However, I prefer to base the river reference on several sites, instead of the best site, to avoid impact from unknown factors, e.g. proximity to spawning sites or that source to sink-dynamics impact densities through proximity to high quality parr habitat. To avoid that the proximity to spawning sites would have high influence on the parr densities in the nursery sites in the river, all of the studied nursery sites are within the main spawning area in river Vindelälven (Östergren 2003).

A flaw in the nursery site inventory method used in the river is that the area that was sampled for habitat characteristics most likely covered a larger area than what the electro fishing could cover. Hence, the habitat mapping may not accurately reflect the area that was electro fished, making the comparison with parr densities less valid.

**Spawning sites**

*Depth and velocity comparison*

There was a significant difference in depth between the spawning sites in the river and the restored spawning beds in the tributaries, suggesting depth to be a limiting variable if salmons were to spawn in the tributaries. However, several other studies report salmon to spawn at depths comparable to what is available in the tributaries, e.g. salmons are known to spawn at lower depth, particularly in smaller watercourses (Loughi et al. 2008; Beland et al. 1982; Moir et al. 2001). The reason none of the radio-tagged salmons in the main stem chose to spawn at shallower depth might simply be due to that there are much more high quality spawning habitats (in terms of substrate and velocity) available in deeper parts of the main stem.

Tributaries and the river reference showed no significant differences in water velocities over spawning beds. The velocities at 30 cm from the bottom were used and therefore it is slightly hazardous to compare velocities from this study with reported spawning bed velocities from other papers, which in general have measured velocities at other depths. The purpose of
measuring the velocity close to the bottom was to measure velocities which salmon are exposed to during spawning (Jones & Ball 1954). Even if differences in methodology are considered, the velocities observed in this study fit well to the velocities presented in the literature (Moir et al. 2001; Beland et al. 1982; Loughi et al. 2008). Hence, salmon are known to spawn in all the velocities occurring at the restored spawning beds in the tributaries. A methodological concern regarding this data is that the velocities are extrapolated and are not actual velocity measurements. Therefore it is hard to know whether the data represent the true velocities at the different sites.

Substrate comparison

The substrate data between tributary spawning sites and river reference had a mean overlap of 27.9%. The overlap did only consist of smaller substrates (< 128 mm). The river reference had a much larger range of different substrate sizes compared to the restored tributary spawning beds, and the average gravel size were considerably smaller in the restored spawning beds compared to the river reference. This suggests that the quality of the restored spawning beds could be considered low with regards to the needs of Atlantic salmon. However, earlier studies have reported salmon to spawn on gravel sizes similar to what is observed in the restored tributary spawning beds (Louhi et al. 2008; Moir et al. 2001), suggesting that salmon may utilize a large range of substrate size for spawning. Still, my results suggest that including larger substrates in the restored spawning beds would probably make the beds more suitable for salmon spawning.

In the spawning survey the radio tagged salmons were tracked to spawning sites. The salmon were assumed to spawn if they were at the same location over a longer period of time in late October. This is a rough assumption. Even if radio tagged salmon spawn in the area where they were holding, it is not certain that the spawning occurred on the exact locations they were tracked to. Further the precision of the tracking varied, up to 100 m² and habitat might differ substantially over such a large area. Due to these reasons it is not certain that it was the actual spawning sites that were measured. To remedy these problems in similar studies I suggest tagging the salmons with activity transmitters and implement intense tracking during the spawning period. With such a method, the salmon will be located with higher precision to the actual spawning sites. An additional methodological concern is that the spawning beds in the tributaries were inventoried in the beginning of October, while salmon spawning primarily occur in mid to late October. Therefore the depths and velocities measured at the spawning beds may not reflect the actual conditions that will be present when they actually spawn.

Conclusions

In conclusion, this study provides a strong indication that salmon parr can inhabit restored tributaries. The habitat characteristics of tributary nursing sites are very similar to those found in the river. There is no clear indication if the spawning prerequisites are fulfilled or not in the restored tributary spawning beds, as the habitat use in the main stem has very little similarity with the restored spawning beds. However, according to several other studies which have investigated salmon spawning habitat, the restored tributary spawning beds do contain the
necessary prerequisites for salmon to spawn, regarding depths, velocities and substrate composition. Further, this study suggests caution against the use of general suitability indexes as a measure to categorize the quality of river habitat to contain salmon parr.

If the number of returning salmons continue to increase in river Vindelälven, it is likely that the salmon will start to utilize parts of the tributaries to a higher degree, both as nursing and spawning grounds. This study can conclude the prerequisites for salmon to utilize the tributaries as nursing grounds are fulfilled. However, it remains slightly unclear whether spawning prerequisites are fulfilled in these tributaries.

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Appendix 1 Velocity overlaps between river reference and restored nursery sites in the tributaries. Dark blue bars, river reference; medium blue bars, tributary; light blue bars, overlap. The graphs are sorted in the order Olsbäcken, Abmobäcken, Gargån, Beukabäcken, Mattjokkbäcken, Rågobäcken, Bjurbäcken, Mösupbäcken, Falåströmbäcken and Hjuksån.
Appendix 2 Depth overlaps between river reference and restored nursery sites in the tributaries. Dark blue bars, river reference; medium blue bars, tributary; light blue bars, overlap. The graphs are sorted in the order Olsbäcken, Abmobäcken, Gargån, Beukabäcken, Mattjokkbäcken, Rågobäcken, Bjurbäcken, Mösupbäcken, Falåströmbäcken and Hjuksån
Appendix 3 Substrate overlaps between river reference and restored nursery sites in the tributaries. Dark blue bars, river reference; medium blue bars, tributary; light blue bars, overlap. The graphs are sorted in the order Olsbäcken, Abmobäcken, Gargán, Beukabäcken, Mattjokkbäcken, Rågobäcken, Bjurbäcken, Mösupbäcken, Falåströmbäcken and Hjuksån.
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