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Spawning site selection of brown trout in habitat restored streams

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Öringens val av lekhabitat i restaurerade bäckar

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Abstract

During the timber floating era, most of Sweden's watercourses were altered. This decreased the amount of available spawning habitats for salmonids, and hence had a negative effect on the riverine brown trout (*Salmo trutta*) populations. Reconstruction of spawning grounds is today a common measure in restoration of altered streams in Sweden. However, very little evaluation of the effectiveness of these reconstructed spawning grounds exists. Hence, today we lack knowledge on how to further improve the construction of spawning habitats.

In this study, conducted in boreal streams in northern Sweden, I have investigated the influence of several variables believed to have importance in spawning habitat selection for brown trout. I have investigated variables at two different scales, the patch scale (the microhabitat where the fish are spawning) and the bed scale (the macrohabitat that surrounds the spawning bed). My results suggest that the percentage of fines within the spawning substrate is an important predictor on probability of spawning at the patch scale. I also report moderate influence of water velocity, area and depth on probability of spawning at the patch scale. Distance to shore were found to have some influence on the selection of spawning bed by trout, while distance to cover for adult spawners, as well as distance to, and size of, nursery habitat were found to have low importance.

To apply these findings for fish and wildlife managers I point out that raking and cleaning of gravel, and the placement of spawning beds further away from shore may be important measures to enhance the probability of spawning in reconstructed spawning habitats.

Sammanfattning

De flesta av Sveriges vattendrag blev förändrade under flottningsepoken. Detta minskade mängden tillgängliga lekområden för salmonider och det hade därmed en negativ effekt på öringspopulationerna (*Salmo trutta*) i vattendragen. Idag är återuppbyggnad av lekbottnar en vanlig del i restaureringen av påverkade svenska vattendrag. Uppföljningar av uppbyggda lekbottnar har utförts i begränsad omfattning och därför saknar vi idag kunskapen för ytterligare förbättring av lekbottenrestaureringen.

I denna studie, utförd i boreala vattendrag i norra Sverige, har jag undersökt påverkan från olika variabler som tros vara viktiga i valet av lekområde för öring. Jag har undersökt variabler i två olika skalor, lekbåsskalan (mikrohabitatet där fisken leker) och lekbottenskalan (makrohabitatet som omger en lekbotten). Resultatet visade att procentuellt inslag av finpartiklar i substratet är en indikation för sannolikhet till lek i något bås. Jag fann även att vattenhastighet, båsets area och djup hade moderat inverkan på sannolikheten till lek i något bås. Avstånd till närmsta strand visade sig ha viss påverkan på lekbottenselektion hos öring, medan avstånd till skydd för lekfisk likväl som avstånd, och area, av yngelhabitat visade sig ha liten påverkan.

För att applicera detta för fiskförvaltare vill jag påpeka att krattning och städning av lekgrus och placering av lekbottnar längre från stranden i bäcken kan vara viktiga åtgärder för att öka sannolikheten till lek i ett rekonstruerat lekhabitat.

Introduction

During the timber floating era in the 19'th and 20'th centuries most of Sweden's rivers and their tributaries were exploited in order to facilitate transportation of timber (Näslund 2000; Törnlund and Östlund 2002; Nilsson et al. 2005). Over 30 000 km of Sweden's watercourses were channelized (Törnlund 2002; Nilsson 2007), as large wooded debris (LWD) and boulders were removed from the rivers, side channels were closed and river banks were reinforced (Lepori et al. 2005; Nilsson 2007). In many cases, channelization had a negative effect on the aquatic ecosystem and in particular on the riverine salmonid populations (Näslund 1999; 2000). Apart from the reduction in suitable feeding habitats and cover (Lepori et al. 2005) removal of impounding structures also increased the water current which made the spawning substrate to either drift away, or get pushed under large boulders (Nilsson 2007; Palm et al. 2007). As a consequence, suitable spawning habitats became spares in many of the channelized boreal rivers (Merz et al. 2004). Lack of spawning habitats may be a strong limiting factor in many salmonid populations (Rubin et al. 2004; Louhi et al. 2008; Sear et al. 2008), decreasing the carrying capacity of the environment and hence the size of the population.

Increased knowledge of the importance of stream heterogeneity (Cooper et al. 1997; Brown 2003) has led to an increased effort to restore streams and their fish populations (Roni et al. 2002; Muotka and Syrjänen 2007). Commonly, LWD and boulders were put back into the water, embankments were removed and closed side-channels reopened (Roni et al. 2002; Palm 2007; Kemp 2010). Although such measures increased habitat complexity and availability, few of the early restoration projects focused on restoration of spawning habitats (Palm et al. 2007). Suitable spawning gravel is essential to salmonid reproduction by providing cover and oxygen supply for eggs and alevins (Kondolf et al. 2008). However, recruitment of new gravel in channelized streams is sparse (Palm et al. 2007) making restoration of spawning habitats an important necessity. Hence, today reconstruction of spawning habitats is a fundamental part in restoration of channelized streams in Sweden and the main feature of such restoration is to make suitable gravel available for fish. However, Palm et al. (2007) state that there are few occasions where the success of the restoration has been evaluated.

Anecdotal evidence has since long pointed to a variation in the utilization of reconstructed spawning beds by the fish (Palm pers. comm. 2011; Ågren pers. comm. 2011). Some spawning beds are used, while others are not. Up until now, no investigation of the potential factors underlying such habitat selection has been undertaken in Sweden. Hence, even though thousands of spawning habitats have been restored and reconstructed since the mid 90´s (see "Åtgärdsdatabasen", county boards) we currently do not know what techniques or strategies work better than others. We therefore lack the knowledge to further improve restoration of spawning beds. Naturally, an evaluation of the effectiveness of spawning ground restoration should begin by investigating what parameters influencing spawning habitat choice by the fish.

Depth, water velocity and substrate size may be important features when it comes to finding the right spawning habitat for the fish (Armstrong et al. 2003; Morbey and Hendry 2008) and previous studies shows what the preferences in these variables salmonids might have (Shirvell and Dungey 1983; Kondolf and Wolman 1993; Nika et al. 2011). Depth influence the probability of stranding of adult fish (Quinn et al. 2001) and bottom freezing during winter effecting survival of eggs (Nika et al. 2011). Water velocity influence energy costs for adult fish during spawning and the accessibility of a spawning patch (Beechie et al. 2008). Substrate influence egg and alevin survival (Kondolf et al. 2008).

Substrate, depth and velocity are all characteristics specific to the spawning patch. However, Sear et al. (2008) suggests that we also have to look at a wider perspective in order to fully understand spawning habitat selection by salmonids, i.e. start to look at variables in the surroundings. Surprisingly, very few studies have so far attempt such a perspective, even though one can suspect many parameters not specific to the spawning patch to have considerable influence on important parameters, such as egg and fry survival.

The time after emergence from the gravel is a critical time for the fry and mortality can be very high as fry disperse and drift downstream searching for a suitable nursery habitat (Elliott 1989; Armstrong et al. 2003). Shorter distance to nursery habitat can reduce mortality amongst emerging fry (Elliott 1987) and this nursery habitat has to be large enough not to risk density-dependent mortality which appears at this early life stage (Elliott 1989). Hence, selecting spawning habitats in close proximity to a big downstream nursery habitat may potentially generate higher survival of the fry and hence be selective (natural selection) advantage for the salmonid.

Also proximity to deep pools and cover for the adult spawners may be an important feature in spawning habitat selection (Armstrong et al. 2003; Rubin et al. 2004). The digging can take several days and therefore both males and females rest in deep water (Armstrong et al. 2003; Nika et al. 2011). Cover in the vicinity of the spawning ground saves energy for the spawners (Nika et al. 2011) and protect the spawners from predators (Bjornn and Reiser 1991; Crisp 1996). Also, position of the spawning bed within the stream may affect choice of spawning habitat (Nika et al. 2011).

The aim of my study is to analyze which variable or variables that are important in the selection of spawning habitat for salmonids, focusing both on variables characterizing the specific spawning patch, as well as variables in the environment surrounding the patch. With the received knowledge, fish and wildlife managers may be able to design and construct more efficient spawning habitats. The study is conducted in three tributaries of river Vindelälven.

Materials and methods

Study sites

The study took place in three different tributaries of river Vindelälven (county of Västerbotten); Beukabäcken (N: 7240543; E: 645158), Nackbäcken (N: 7191291; E: 692524) and Tväråbäcken/Västibäcken (N: 7195356; E: 659994) (all coordinates are according to SWEREF 99TM) (Figure1.). The river Vindelälven and its tributaries are part of a Natura 2000 area. Beukabäcken and Nackbäcken have direct contact with river Vindelälven while Tväråbäcken/Västibäcken runs out into the lake Falträsket in the Vindel river catchment area. The flow in the streams during the time of study varied between 0.67-1.86 m^3/s in Beukabäcken, 2.08-2.93 m^3/s in Nackbäcken and 0.57-0.80 m^3/s in Tväråbäcken/Västibäcken. Water temperature varied from 9ºC at the beginning of the study, to 3ºC at the end of the field study. Brown trout is both stationary and migratory in these streams, and the spawning period takes place in the beginning of October. The average 0+ density of brown trout is 6.0 in Beukabäcken, 6.7 in Nackbäcken and 3.3 in Tväråbäcken/Västibäcken (data from the last electrofishing occasion derived from SERS 2012). Other fish species that occurs in the streams are pike (*Esox lucius*) and burbot (*Lota lota*). Also, brook lamprey (*Lampetra planeri*) is found in Nackbäcken, and grayling (*Thymallus thymallus*) and Atlantic salmon (*Salmo salar*) in Beukabäcken (SERS 2012). The surroundings of the streams are mainly cultivated forest of Norwegian spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), and the riparian zone mostly consisting of scattered deciduous trees, such as birch (*Betula spp.*), grey alder (*Alnus incana*) and willow (*Salix spp.*).

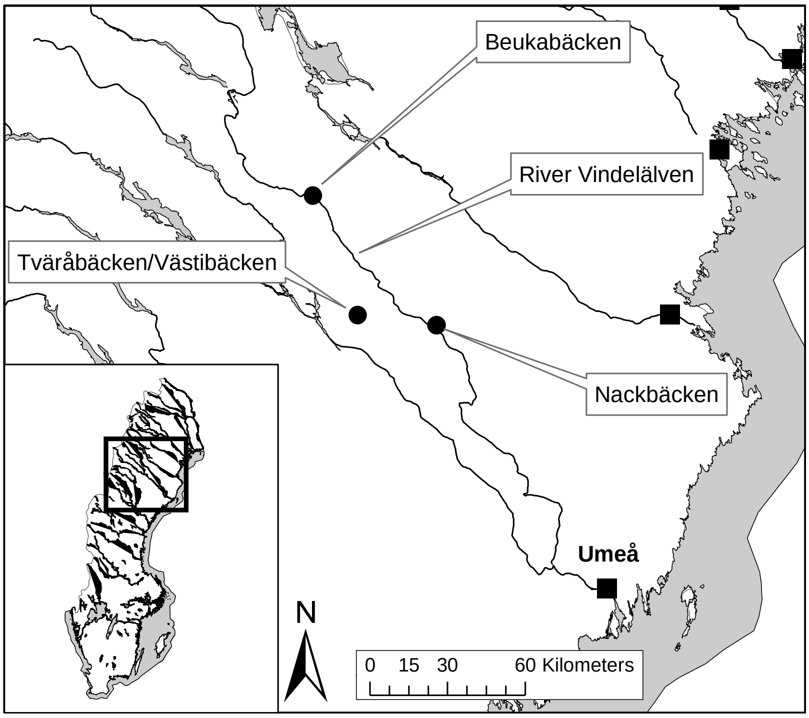

Figure 1. Map showing the positions of the tributaries investigated in this study.

All three of these tributaries were affected by channelization during the timber floating era, resulting in a decreasing availability of feeding and spawning habitats for the salmonid populations. During the restoration projects large stones and boulders were brought from the banks and placed, at random, back in the stream. Natural structures such as pools and weirs were strengthened. Spawning habitats were reconstructed in all three streams. The restorations took place between 2004 and 2011.

Most of the spawning beds at the study sites were constructed according to the Hartijokki method (Degerman 2008). The Hartijokki method use already existing gravel for the restoration of the spawning beds. The stones and boulders of the stream floor are loosened to get access to the under-laying gravel. The gravel was being coarsely filtered to sizes < 5 cm, before being secured with larger stones and boulders, creating the typical "horseshoe" structure of a Hartijokki spawning bed (Figure 2). It is in these "booth-like" spawning patches that the salmonids are spawning. Several Hartijokki "booths" can be constructed on one bed of gravel (Figure 2.). The placement of the beds in the stream is often based on a subjective assessment of suitable water velocities and depth.

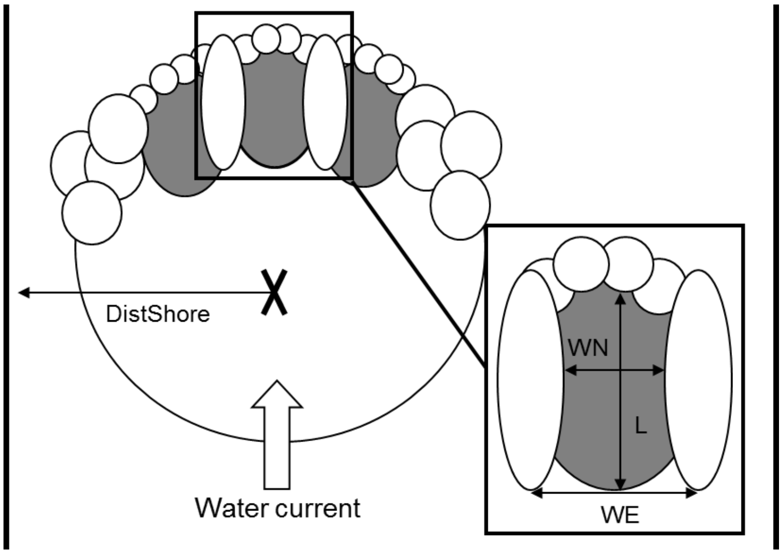

Figure 2. Illustration of a spawning *bed*, containing three spawning *patches* of Hartijokki-type. The grey shaded area shows the patch where spawning occurs. Larger stones secure the spawning gravel from dispersal downstream. DistShore were measured from the center of the spawning bed to the nearest shore. The superimposed picture show how length, L, and width, WN and WE, were measured on the patch.

A few “spawning-booths” were also constructed on beds of external gravel, i.e. instead of using gravel extracted from the river bottom, already filtered gravel acquired from a stone quarry were used.

This study will hereafter distinguish between “spawning beds” and “spawning patches”. Spawning beds are defined as beds of gravel, upon which one or several spawning patches are placed. Spawning patches are defined as small, often booth-like structures, in where the spawning takes place.

Field survey

The fieldwork was conducted during September and October in the autumn of 2011, where some of the data was collected before the spawning period and some was collected after the spawning had taken place. Before all measurements started, all spawning beds were located with the help of coordinates from earlier restoration projects. Mapping and measurements of spawning habitats were conducted on two different scales, *patch* scale representing the micro-habitat at the actual gravel-patch where spawning occur, and *bed* scale representing the macro-habitat surrounding the patch. Table 1 summaries the number of beds and patches sampled in the study, as well as the characteristics of the variables measured.

Table 1. Summary statistics of number of beds and patches sampled in the study, as well as the characteristics of all variables measured (mean ± standard deviation).

(Mean±Standard deviation)	Beukabäcken	Nackbäcken	Tväråbäcken/ Västibäcken	All streams together
Spawning patch (N)	96	43	26	165
Percentage of fines (%)	1.82±1.84	7.84±12.01	2.79±1.91	3.55±6.79
Water velocity at half depth (m/s)	0.51±0.12	0.52±0.15	0.40±0.10	0.50±0.13
Water velocity near bed (m/s)	0.37±0.10	0.28±0.16	0.31±0.10	0.34±0.12
Water depth (m)	0.49±0.09	0.62±0.16	0.41±0.10	0.51±0.13
Area of spawning patch (m^3)	0.34±0.13	0.53±0.40	0.80±0.32	0.46±0.31
Spawning bed (N)	31	14	10	55
Distance to cover upstream (m)	4.43±6.77	3.01±2.46	40.47±45.63	10.62±24.00
Distance to cover downstream (m)	7.95±6.28	9.85±6.78	46.25±46.98	15.40±24.84
Distance to nursery habitat (m)	3.77±7.83	2.15±5.00	6.47±13.05	3.88±8.44
Area of nursery habitat (m^3)	41.58±74.16	45.79±41.62	140.50±261.08	60.64±127.59
Distance to nearest shore (m)	2.94±1.06	3.58±1.27	2.34±0.82	3.03±1.14

Variables measured on Spawning patch

Occurrence of eggs was carefully checked at each patch. Two persons using aquascopes observed the patch while one of them gently scraped the gravel and the other held a fine meshed net downstream the patch. Occurrence of at least one egg, either sighted using aquascope, or collected in the mesh net, confirmed that spawning had occurred at the patch.

Length (L) (cm) and width (cm) of each spawning patch was measured. The width was taken both at the upstream entrance of the patch (WE) and at the most narrow point (WN). With these parameters I could calculate the area (m^2) for each patch by using the mean of the widths multiplied with the length ((WE + WN) / 2 * L) = Area) (Figure 2.).

Water velocity (m/s) was measured at two depths, near bed (VelBottom) and at half depth (VelHalf). Velocity was measured using an electromagnetic flow metre (Valeport 801, Townstal Industrial Estate, Dartmouth, U.K.) The depth of each spawning patch was measured at the center of the upstream entrance of each patch.

A sample of substrate was collected from each spawning patch. Back at the lab the samples of gravel was dried and then separated in fractions using sieves of 5 sizes, 16mm, 5.6mm, 1.6mm, 1.0mm and 0.56mm (Palm et al. 2007). The fraction >16mm were excluded, not to achieve bias from very large fraction. The remaining 5 fractions (16-5.6mm, 5.6-1.6mm, 1.6-1.0mm, 1.0-0.56mm and <0.56mm) were weighed and the percentage towards the total weight was calculated. Each fraction of substrate were weighed to the nearest 0.1 g. Fractions below 1.0mm, are often defined as “fines” (Crisp 1996). To investigated the influence of fines in substrate composition, I used the added percentage of the two lowest fractions (1.0-0.56mm and <0.56mm) as a variable in further analysis.

Variables measured on Spawning bed

The position of the spawning bed was recorded by measuring the distance to each shore, and selecting the shortest distance of these two in order to get the minimum distance to shore (DistShore) (Figure 2.).

Distance to suitable downstream nursery habitat for the fry (DistNursery) was measured for each bed. The area of the nursery habitat was also measured (AreaNursery). Optimal nursery habitat was defined as shallow (<30 cm), fairly slow-running water (i.e. no white water) with plenty of stones and boulders for the fry to hide among (Armstrong et al. 2003). If the nursery habitat was immediately adjacent to the spawning ground the distance was recorded as 0.

Cover was defined as an area with water deeper than 50 cm and big enough to hide an adult spawner (Nika et al. 2011). In places >50cm with higher water velocities, the area should be in immediate connection to LWD or boulders in order to be classified as cover. Distance to upstream and downstream cover was measured (DistUpCover, DistDownCover).

Area, DistShore, DistNursery, AreaNursery, DistUpCover and DistDownCover were collected before spawning, and Depth, VelBottom, VelHalf and FineSub were collected after spawning.

Analysis

Utilization of patch was defined as the occurrence of eggs in the gravel. Utilization of beds was defined as occurrence of eggs in at least one of the patches in the bed. 34 out of 165 patches and 26 out of 55 beds contained eggs (Table 2.). I wanted to explain the variation in the utilization of bed or patch using the explanatory variables described above. To do this I applied statistical modeling. I analyzed spawning patch variables and spawning bed variables separately.

Table 2. Summary statistics of number of beds and patches sampled in the study, as well as the characteristics of all variables measured (mean ± standard deviation), divided on patches and beds where egg occurred or not.

(Mean±Standard deviation)	No egg occurrence	Egg occurrence
Spawning patch (N)	131	34
Percentage of fines (%)	3.94±7.47	2.06±2.47
Water velocity at half depth (m/s)	0.51±0.13	0.45±0.13
Water velocity near bed (m/s)	0.35±0.12	0.32±0.14
Water depth (m)	0.50±0.12	0.55±0.16
Area of spawning patch (m^3)	0.41±0.26	0.64±0.40
Spawning bed (N)	29	26
Distance to cover upstream (m)	3.50±2.46	3.28±2.89
Distance to cover downstream (m)	6.98±4.19	7.12±4.54
Distance to nursery habitat (m)	1.40±2.22	1.09±2.95
Area of nursery habitat (m^3)	31.46±25.09	43.73±40.39
Distance to nearest shore (m)	2.75±0.81	3.51±1.06

Data exploration

In order to meet the assumptions of parametric linear regression I carefully explored the data. Collinearity between explanatory variables was evaluated using pair-wise scatter-plots and Pearson correlation coefficients. There was low to moderate correlation between all combination of variables ($r^2 < 0.4$) (Appendix 1 and 2). If the correlation between explanatory variables is higher than 0.6, Zuur et al. (2009) recommend that only one of the variables should be used in the analysis (as the two variables will roughly explain the same variation in the data).

The normality assumption on the raw variables was investigated using histograms (Appendix 1 and 2). As I used logistic models (i.e. a binomial distributed response variable, see below), normality was only checked on the explanatory variables. Substrate was found to be heavily skewed and was hence square root transformed. This action also reduced the influence of outliers.

Linearity between the response and the explanatory variables were investigated using generalized additive models. A mild degree of non-linearity could be established for DistUpCover and AreaNursery, but as the non-linearity was weak I choose to not model these terms as polynoms.

Outliers were checked using scatterplots. Several of the explanatory variables measured on the scale of bed contained extreme observations. Transformation did not reduce the influence of these observations, and I hence choose to remove them from the analysis. Unfortunately, as several of these extreme observations were evenly dispersed over many beds (mainly in Tväråbäcken/Västibäcken), 16 beds had to be removed from the data. This resulted in a 30% reduction of the spawning bed data.

Statistical modeling

Probability of spawning at the level of patch (i.e. occurrence of eggs) was modeled as a function of Area, VelBottom, VelHalf, Depth and FineSub, using a generalized linear mixed effect model with binomial errors and a loglink function. "Stream" was incorporated as a random effect in the model to account for possible pseudoreplication (i.e. to handle within-stream correlations of observations). In total, 32 models were created containing all possible combinations of the fixed effect variables, each model reflecting a hypothesis about the relationship between the response variable and the explanatory variables. An empty model, with no explanatory variables included, was used as a "null hypothesis" representing no effect of the explanatory variables. Care was taken not to overparameterize the models, and I followed Anderson (2008) recommendation that the number of models tested should not exceed the number of data points. An information theoretic approach (Burnham and Anderson 2002) was used to rank models, using Akaike Information Criteria adjusted for small sample size (AICc). Besides AICc ranking, support for models was expressed in terms of model probabilities (Akaike Weights) (Burnham and Anderson 2002; Anderson 2008) and evidence ratios. Akaike weights quantify the probabilities that a model is the best model, given the data and the model set. Evidence ratios are the ratio between two model probabilities and give a measure of the relative support of one model compared to the other model. Effect of variables was based on their importance values (Anderson 2008). Importance values represent the overall support for each variable across all models and are calculated as the sum of the Akaike weights of all models containing the variable (Calcagno 2011).

An identical modeling approach was used to model the probability of spawning at bed level as a function of DistShore, DistNursery, AreaNursery, DistUpCover and DistDownCover.

All analysis and data exploration was performed in the statistical program R (R Development Core Team 2011) using the packages lmer (Bates and Meachler 2011) glmmulti (Calcagno 2011); mcgv (Wood 2006) and AED (Zuur et al. 2009).

Results

In the model selection on the patch scale 32 models were created, representing all possible combinations of the five explanatory variables used, plus one empty model. My analysis showed that the model which contained Depth+Area+VelHalf+FineSub was the best model with the lowest AICc (Table 3.). This model was 244 times more likely to be the most parsimonious model compared to an empty model (indicating strong effect of variables on probability of spawning), but only 1.2 times more likely than the next best model (indicating model selection uncertainty).

Table 3. The 95 % confidence set of ordinal logistic regression models testing the effect of explanatory variables on spawning probability at the patch scale. Model selection was conducted using second order Akaike Information Criteria on a set of 32 models (representing all possible combinations of the explanatory variables), as well as one common intercept model (“no effect” model). Support for models is expressed as delta AICc and AICc weights. Percentage of fines in substrate (FineSub), water depth (Depth), area of spawning patch (Area), water velocity at bottom (VelBottom) and water velocity at half depth (VelHalf) were the five explanatory variables included in the model selection.

Model	AICc	ΔAICc	AICc weights	Rank
Depth+ Area+ VelHalf+ FineSub	156.19	0	0.12	1
VelHalf+ FineSub	156.52	0.33	0.10	2
Depth+ Area+ FineSub	156.79	0.60	0.09	3
Depth+ VelHalf+ FineSub	156.84	0.65	0.09	4
Area+ VelHalf+ FineSub	157.40	1.21	0.07	5
Depth+ FineSub	157.53	1.34	0.06	6
FineSub	157.70	1.51	0.06	7
Depth+ Area+ VelBottom+ VelHalf+ FineSub	157.78	1.59	0.06	8
Area+ FineSub	157.81	1.62	0.05	9
Depth+ VelBottom+ VelHalf+ FineSub	158.35	2.16	0.04	10
VelBottom+ VelHalf+ FineSub	158.51	2.32	0.04	11
Depth+ Area+ VelBottom+ FineSub	158.77	2.58	0.03	12
VelBottom+ FineSub	159.15	2.96	0.03	13
Area+ VelBottom+ FineSub	159.17	2.98	0.03	14
Depth+ VelBottom+ FineSub	159.50	3.31	0.02	15
Area+ VelBottom+ VelHalf+ FineSub	159.60	3.41	0.02	16
Area+ VelHalf	160.33	4.14	0.02	17
Depth+ Area+ VelHalf	160.34	4.15	0.02	18

Percentage of fines in substrate had the highest relative importance value (0.92) out of the explanatory variables used (Table 4.) and a model containing FineSub as the only variable was 148 times more likely being the most parsimonious model compared to an empty model. FineSub had a negative relationship with probability of spawning on a patch (Figure 3.). VelHalf, Depth and Area all had moderately high relative importance values ranging from 0.55-0.59 (Table 4.), Area and Depth had a positive relationship, while VelHalf had a negative relationship with probability of spawning on a patch (Figure 4.). VelBottom had a low relative importance value (0.30) and was hence considered to have little effect on probability of spawning.

Table 4. Relative importance of the explanatory variables at the patch scale based on importance values (Anderson 2008).

	Importance value
FineSub	0.92
VelHalf	0.59
Depth	0.56
Area	0.55
VelBottom	0.30

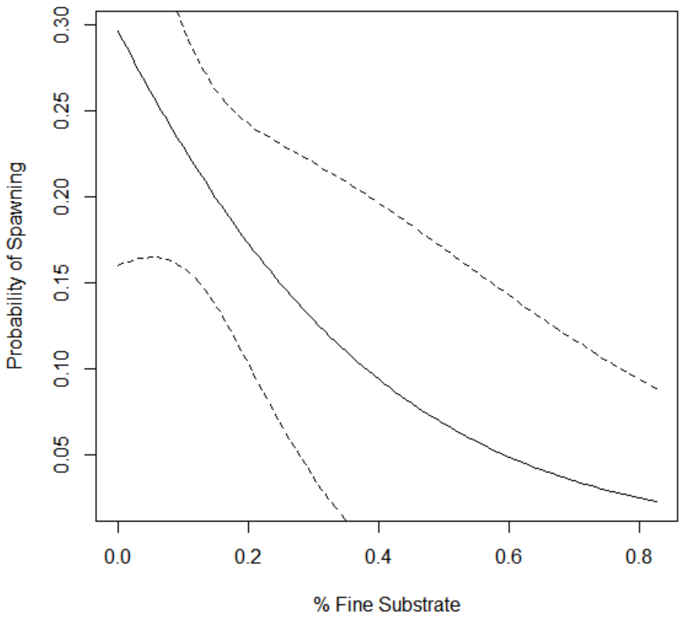

Figure 3. The relationship between the percentage of fines in substrate (x-axis) and the probability of spawning. Probability estimates are model averaged. The dashed lines are showing 95% confidence limits.

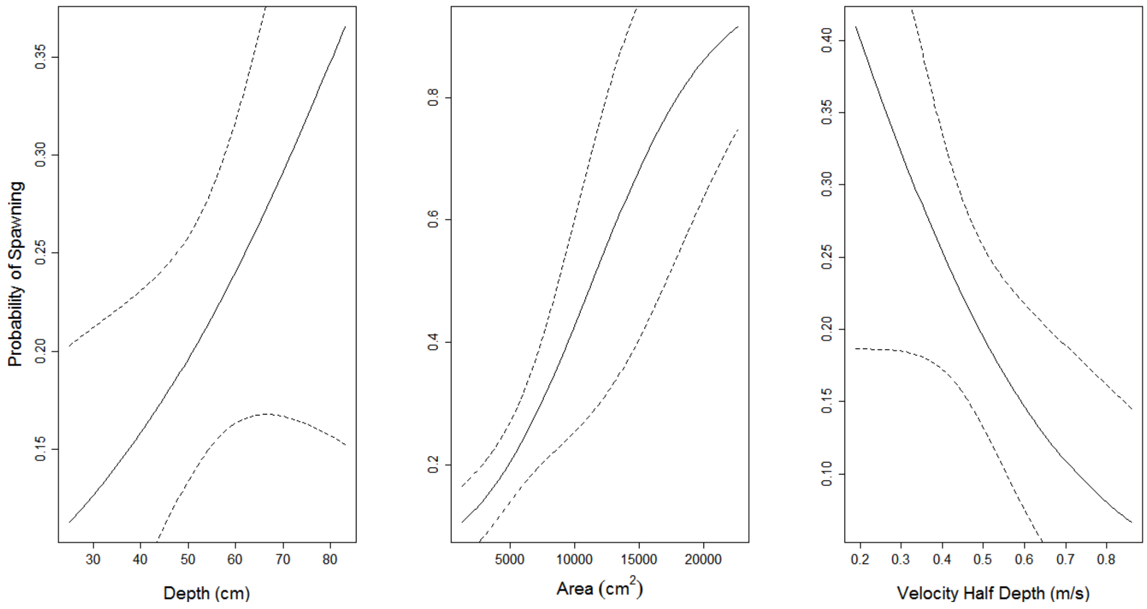

Figure 4. The relationships between Depth, Area of spawning patch and Water velocity at half depth (x-axis, respectevly) and the probability of spawning. Probability estimates are model averaged. The dashed lines are showing 95% confidence limits.

In the model selection at the bed scale there was 32 models created, representing all possible combinations of the five explanatory variables used, plus one empty model. My analysis showed that the model which contained only DistShore were the best model with the lowest AICc (Table 5.). This model was 5.7 times more likely to be the most parsimonious model compared to an empty (indicating a weak effect of variables on probability of spawning), and 2.7 times more likely than the next best model (indicating model selection uncertainty).

Table 5. The 95 % confidence set of ordinal logistic regression models testing the effect of explanatory variables on spawning probability at the bed scale. Model selection was conducted using second order Akaike Information Criteria on a set of 32 models (representing all possible combinations of the explanatory variables), as well as one common intercept model (“no effect” model). Support for models is expressed as delta AICc and AICc weights. Shortest distance to shore (DistShore), distance to nursery habitat (DistNursery), area of nursery habitat (AreaNursery), distance to upstream cover (DistUpCover) and distance to downstream cover (DistDownCover) were the five explanatory variables included in the model selection.

Model	AICc	ΔAICc	AICc weights	Rank
DistShore	52.29	0	0.27	1
AreaNursery+ DistShore	54.18	1.89	0.11	2
DistDownCover+ DistShore	54.32	2.03	0.10	3
DistNursery+ DistShore	54.54	2.25	0.09	4
DistUpCover+ DistShore	54.78	2.49	0.08	5
“Empty model”	55.87	3.58	0.05	6
DistDownCover+ AreaNursery+ DistShore	56.62	4.34	0.03	7
DistUpCover+ AreaNursery+ DistShore	56.64	4.35	0.03	8
DistNursery+ AreaNursery+ DistShore	56.75	4.47	0.03	9
DistDownCover+ DistNursery+ DistShore	56.88	4.59	0.03	10
DistUpCover+ DistDownCover+ DistShore	56.92	4.63	0.03	11
AreaNursery	57.17	4.88	0.02	12
DistUpCover+ DistNursery+ DistShore	57.18	4.89	0.02	13
DistUpCover	58.12	5.84	0.01	14
DistNursery	58.12	5.84	0.01	15
DistDownCover	58.19	5.91	0.01	16
DistUpCover+ AreaNursery	59.15	6.86	0.01	17
DistUpCover+ DistDownCover+ AreaNursery+ DistShore	59.21	6.92	0.01	18
DistDownCover+ DistNursery+ AreaNursery+ DistShore	59.41	7.12	0.01	19

Shortest distance to shore (DistShore) had the highest relative importance value (0.84) out of the explanatory variables used (Table 6.) and a model containing DistShore as the only variable was 5.7 times more likely being the most parsimonious model compared to an empty model. DistShore had a positive relationship with probability of spawning on a bed (Figure 5). The other four explanatory variables had low relative importance values ranging from 0.22-0.28 (Table 6.).

Table 6. Relative importance of the explanatory variables at the bed scale based on importance values (Anderson 2008).

	Importance value
DistShore	0.84
AreaNursery	0.28
DistDownCover	0.24
DistNursery	0.23
DistUpCover	0.22

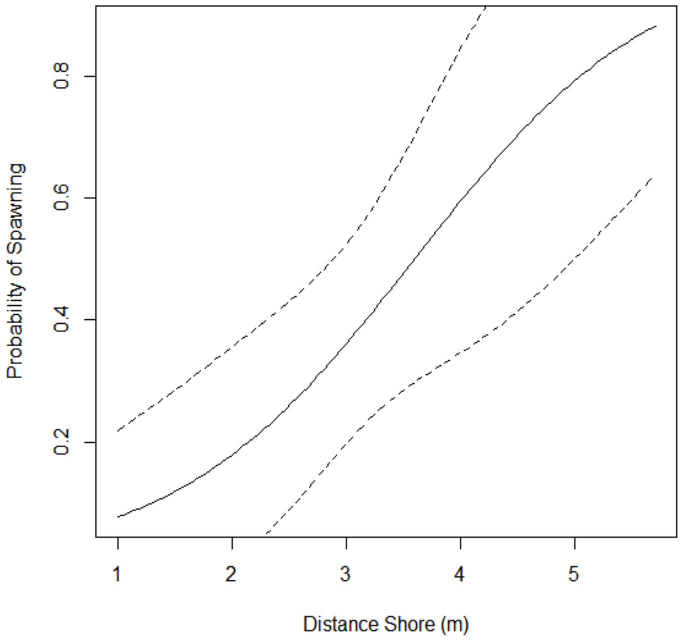

Figure 5. The relationship between the distance to nearest shore (x-axis) and the probability of spawning. Probability estimates are model averaged. The dashed lines are showing 95% confidence limits.

Methological considerations

My analysis is based on model selection using an information theoretic approach (Burnham and Anderson 2002). A big difference from classical (Fisher-based) statistics is that no p-value threshold is used when making statistical inference. Hence, results are expressed in terms of “support in the data” (or “importance”), instead of a simple yes/no (below or above p=0.05).

Model selection based on stepwise (backward or forward) techniques (i.e. starting with the full model and remove variables, or starting with a minimal model and add terms) using likelihood ratio tests has received criticisms, as depending on approach, one may end up with different results. An exhaustive selection approach (i.e. testing all possible combinations of variables) avoids this problem, but such approach demands comparing models that are not nested. Ranking models based on AIC is valid even if models are not nested and are hence suitable strategy.

My model selection resulted in many models with similar weight in the data. Drawing statistical inference based solely on the best ranked model would not reflect such model-selection uncertainty. To account for this, I used model averaging techniques (multimodel-inference) to derive parameter-estimates and to rank importance of variables (Anderson 2008).

Discussion

My result revealed that percentage of fines in substrate (patch scale) and distance to shore (bed scale) were the two most important explanatory variables at the two scales studied. At the patch scale water velocity at half depth, area of patch and water depth showed to be moderately important while velocity at bottom had relatively low importance. At the bed scale the other four explanatory variables (distance to nursery habitat, area of nursery habitat and the distance to cover both upstream and downstream) showed to be of low importance. The discussion mostly focuses on the variables that showed to be important.

Spawning patch

Among the variables used, the analysis ranked the percentage of fines in substrate as the most important variable effecting spawning patch selection. There have been numerous studies investigating the effect of substrate on selection of spawning habitat in salmonids. Substrate is a complex variable and various aspects have been independently studied, such as size of gravel (Kondolf and Wolman 1993), substrate composition (Witzel and MacCrimmon 1983) and the importance of fines (Chapman 1988). My result revealed that a higher percentage of fines in the substrate lowers the probability of spawning at a patch. This is in agreement with Rubin et al. (2004) who report fewer spawning events in stream sections where spawning beds are dominated by fine sediments. Chapman (1988) states that higher percentage of fines in the substrate has negative effect on egg to fry survival. The underlying mechanism behind the avoidance of substrate containing fines may hence be a result of selection pressure against fish spawning in such habitats. In my study, average percentage of fines in substrate was below 5%. In comparison to other studies, this can be considered low, and Crisp et al. (1996) report that <15 % fines in substrate is considered suitable for spawning.

The more the spawning patches are used, the lesser amount of course gravel will be left in the patch, as female digging continuously removes gravel downstream. Hence percentage of fines may increase in substrate, as the ratio of course gravel will decrease. High floods also disperse gravel downstream, which is a general problem for the reproduction of riverine salmonid populations (Barlaup et al. 2008). My result enforces the importance of maintaining constructed spawning habitats by regularly raking and cleaning them.

Shirvell and Dungey (1983) investigates habitat preferences based on substrate (quantified as the mean size of gravel) and water velocity. They analyze the variance of the variables and state that substrate is the most important variable due to less variation. However, they also state that these variables come hand in hand, as they often are highly correlated (i.e. higher velocity equals courser gravel). In my study I could not see any obvious correlation between percentage of fines in substrate and water velocity near bed (a negative correlation of r=0.2; Appendix 1.).

Water velocity near bed was ranked to have low importance on probability of spawning in the statistical analysis. This is in contrast to several other studies that have concluded velocity at bottom as an important variable in spawning habitat selection (Shirvell and Dungey 1983).

Velocity at half depth was ranked moderately important, with a negative relationship between velocity and probability of spawning. Beland et al. (1982) conclude that size-dependent endurance (i.e. larger fish can tolerate larger velocities) may affect the choice of spawning bed. In this study, spawners may not be big enough to tolerate beds with the highest water velocities recorded, explaining the negative correlation seen between probability of spawning and velocity.

Velocity at half depth was ranked more important than velocity at bottom, suggesting that minimizing energy cost of the spawning adults may be more important rather than optimizing the oxygen supply to the egg pocket. An alternative option could be that a wider range of accepted values of velocity at bottom than velocity at half depth occurred in the data, and hence that active selection of water velocities at bottom was not necessary for the fish (hence the low relative importance of velocity at bottom).

Depth was ranked to have moderate importance on probability of spawning, with a positive relationship between depth and probability of spawning. Shirvell and Dungey (1983) found that spawning occur in water depths up to 82 cm, which correlates with my study where depths up to 83 cm were recorded (all patches, both where spawning occurred and not). They also state that spawners compromise preferred water velocities at the bottom in order to find a better depth-velocity combination, when availability of spawning patches with both preferred depth and velocity is insufficient to accommodate all spawners. This correlates with my result revealing that depth has higher importance value than velocity at bottom.

The area of the spawning patch was ranked to have moderate importance, with a positive relationship between patch area and probability of spawning. Few studies have investigated the effect of size of the spawning patch on habitat selection in salmonids. Barlaup et al. (2008) conclude that larger sized trout require larger patches of available gravel. It is likely that large area spawning patches have a higher probability of containing a sufficient thick layer of gravel for the salmonids to be able to dig a deep enough depression. This may hence possibly explain the higher probability of spawning at larger sized patches. Earlier studies look more at the total availability of spawning gravel, rather than looking at the size of each patch.

The four explanatory variables discussed above (Depth, Area, VelHalf, FineSub) are all included in the model that received the highest AICc weight. Even though percentage of fines in substrate is the variable with the highest importance value, this indicates that there are more than one variable involved in the selection of a spawning patch. This is in agreement with Shirvell and Dungey (1983) that state that trout search for an optimum combination of a number of variables rather than a single variable with preferred value.

Spawning bed

At the scale of the spawning bed, shortest distance to shore had the highest relative importance value among the variables studied. My results revealed that the probability of spawning on a spawning bed increased with the distance from the nearest shore, suggesting that spawning beds should be placed in the center of the stream. This variable has not been thoroughly studied earlier, however Zimmer and Power (2006) conclude the placement of spawning beds in the relation to shore to have low importance. The positive relationship between distance to shore and probability of spawning found in my study may be explained by an increased risk of sediment deposition on to the spawning bed due to erosion on the stream bank.

The exposure to predation during spawning may be higher if close to shore. Quinn et al. (2001) found out that salmonids got killed to a greater extent in a narrow river than a wider one, due to bear predation. They conclude that this is due to less escape routes in a narrow river. Hence the same effect may be assumed for a bed close to the shore compared to a bed at the center of the river.

Nika et al. (2011) also measure the distance to shore, same as in this study. However, rather than testing the effect of distances to shore (as done in this study), they analyze the avoidance of shore according to different characters of the bank. However, in contrast to my findings they didn’t find any difference in the placement of the spawning beds (even though we have looked at slightly different aspects). Hence, the effect of the distance to shore needs to be studied further.

All other variables used to explain variation in utilization of spawning beds was ranked low, and hence had little effect on spawning probability. However I don’t state that these variables are unimportant, I state that in comparison to other variables these variables are less important in the selection of spawning beds for salmonids. Cover in the vicinity of spawning bed have been found important in other studies (Armstrong et al. 2003), however my result showed no importance of either upstream neither downstream cover. Nika et al. (2011) conclude that cover at a distance further away than 10 m may be a trade-off between spawning success at preferred bed and energy cost. In my study, few of the covers were further away than 10m from bed, perhaps indicating that the fish did not have to trade energy and cover in the way Nika et al. (2011) proposed. All cover may hence be within acceptable distance to bed, resulting in that no active selection in this variable was made by the fish (i.e. explaining the low importance of the variable).

Distance to nursery habitat showed low relative importance on spawning bed selection. Palm (2005) state that the normal drift distances for dispersing fry is 0-400 m. In my study all recorded values were well within this range (0-10m). Hence, all beds in the study may have an acceptable distance to suitable nursery habitats, and hence that fish did not actively select on this variable.

As one can see in this and previous studies there are a lot of variables involved in the selection of spawning ground, and this may be a complex issue for restoration projects to face.

There could be even other variables that play a big role in the selection of spawning habitat that I have not looked at in this study. If other variables should be included in a future study a larger sample size would be needed to avoid the risk of overparameterization. Variation between rivers should also be considered when planning restoration projects. Due to large volumes of rain fall in the autumn, the streams in the study had very high water levels and this can have had an effect on the result, suggesting that variation between years have to be considered. I suggest that similar studies should be conducted in other streams to validate my results and to see if there are differences in the importance of explanatory variables between rivers. Substrate could be studied on various levels and future studies should study the importance between these levels. The variables used at the spawning bed scale have been studied to a limited extent and I recommend that further studies should not only look at variables at patch scale, but also investigate variables in the surroundings of the spawning bed. In this study percentage of fines in substrate (patch) and distance to shore (bed) had the highest relative importance at the two scales. Comparisons between variables from different scales are something to consider for future studies to get a better understanding of the selection of spawning habitat by salmonids.

In conclusion, this study reported percentage of fines in spawning substrate to have strong effect on the probability of spawning at patch level. Decreasing percentage of fines increases the probability of spawning on a spawning patch. Further, velocity at half depth, area of patch and depth also influence patch selection, area of patch and depth had a positive relationship with probability of spawning while velocity at half depth had a negative relationship. Secondly, distance to shore was found to be the most important variable at the spawning bed scale. Increasing distance to shore increased the probability of spawning. The explanation behind these findings remains unclear and future studies need to be conducted on this issue. For fish and wildlife managers working with trout populations in small to medium sized boreal rivers, I suggested raking and cleaning of the gravel in the constructed spawning habitats, in order to get a lower percentage of fines in the substrate. I also recommend placing the spawning bed further away from shore.

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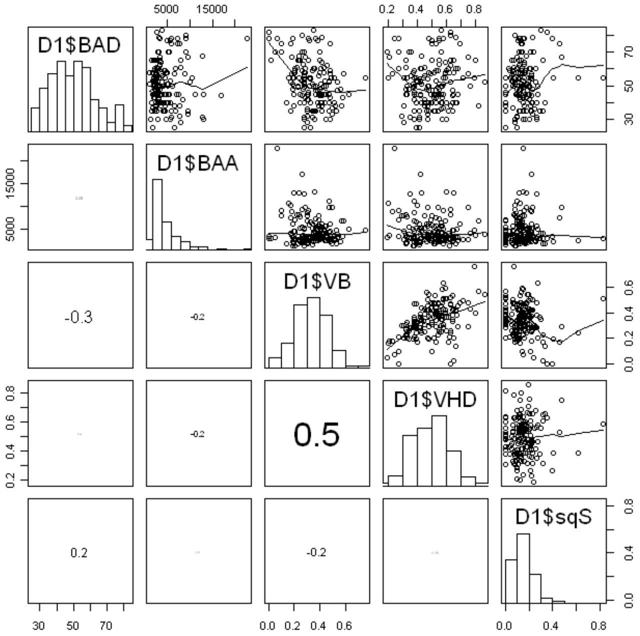
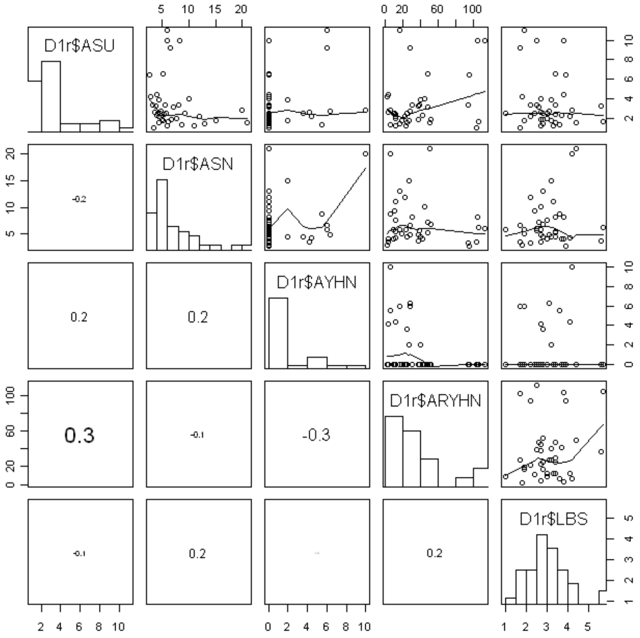
Appendix



Appendix 1. Pair-wise scatter-plot and Pearson correlation coefficients showing the collinearity of the explanatory variables of the patch scale. The histograms at the center shows the normal distribution of the data. The differences in size of the Pearson correlation coefficients is proportional to the strength of the correlation.



Appendix 2. Pair-wise scatter-plot and Pearson correlation coefficients showing the collinearity of the explanatory variables of the bed scale. The histograms at the center shows the normal distribution of the data. The differences in size of the Pearson correlation coefficient is proportional to the strength of the correlation.

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