



# Examensarbete i ämnet biologi

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## Pre-spawning habitat selection of subarctic brown trout (*Salmo trutta* L.) in the River Vindelälven, Sweden

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**Pre-spawning habitat selection of subarctic brown trout  
(*Salmo trutta* L.) in the River Vindelälven, Sweden**

*Habitatval hos stor öring månaden före lek i övre Vindelälven*

**Erik Spade**

Keywords: mapping, stream, depth, velocity, substrate, preference, radio-telemetry, Vindelälven

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## ABSTRACT

Habitat selection of migratory brown trout at the upper reaches of River Vindelälven, was studied in September during the pre-spawning period. The fish migrate from down- or upriver lakes for spawning in the river and data was collected by habitat mapping and radio-telemetry. Habitat selection of fish was analysed with preference curves and statistical modelling, using the physical variables; depth, stream velocity and streambed substrate. Preference curves were derived by comparing fish habitat use with their nearby available environment while the statistical modelling aimed to answer three main questions. 1) Do the trout have a specific preference of depth, water velocity and streambed substrate? 2) Is there any difference in habitat selection between sexes? 3) Is there a shift in habitat selection over time? The preference curves indicated that trout favored water depths of 1-2 m, velocity compositions characterized as glides (c. 0.2-0.4 m s<sup>-1</sup>), both fine (0.02-2 mm) and large (>200 mm) substrate compositions. The overall habitat selection of fish was significantly influenced by all three investigated physical variables. Stream velocity was the only factor statistically segregating females and males in habitat selection, where males used higher velocity areas. No shifts in habitat selection over the one month study period were found. The complexity of streams and correlations between variables often results in difficulties to evaluate fish habitat preferences and consequently future challenges lies in the development of models accounting for a wider range of abiotic and biotic factors.

## SAMMANFATTNING

Habitatval hos vandrande öring, med sitt huvudsakliga utbredningsområde i övre delarna av Vindelälven, studerades under september en månad innan lek. Data på djup, vattenhastighet och bottensubstrat samlades in genom biotopkartering, och telemetristudier visade fiskens ståndplatsval. Öringarnas habitatval analyserades med preferenskurvor, baserade på data av utnyttjande och tillgång av olika habitat, samt statistisk modellering baserat på tre frågor. 1) Har öring en specifik preferens för djup, vattenhastighet och bottensubstrat? 2) Finns det någon skillnad i habitatval mellan könen? 3) Finns det skillnader i val av habitat över tid? Preferenskurvorna indikerade att öringen föredrog djup av 1-2 m, områden med ett dominerande inslag av svagt strömmande vatten (c. 0.2-0.4 m s<sup>-1</sup>), samt bottnar med både fina (0.02-2 mm) och grova (>200 mm) sammansättningar av substrat. Alla tre variabler inverkar signifikant på fiskens habitatval. Vattenhastighet var den enda faktorn som statistiskt skilde könen val av habitat, då hanar föredrog en högre hastighet än honor. Inga skiftet i habitatval i relation till tid, över den månad som studien pågick, var möjliga att urskilja. Komplexiteten i strömmande vatten och en korrelation mellan olika variabler resulterar ofta i svårigheter i att skatta fiskens habitatpreferens, där framtida utmaningar ligger i att utveckla modeller som kan analysera en större mängd abiotiska samt biotiska data.

## INTRODUCTION

Brown trout (*Salmo trutta* L.) is commonly recognized as one of the most studied freshwater fish species and numerous studies have described habitat preferences (e.g. Armstrong et al. 2003, Zimmer & Power 2006, Heggenes & Saltveit 2007), migrations (e.g. Arnekleiv & Kraabøl 1996, Carlsson et al. 2004, Zimmer et al. 2010) and the life history traits (e.g. Jonsson & Sandlund 1979, Jonsson 1989, Elliot 1994, Milner et al. 2003) of various brown trout populations. It is widely accepted that habitat selection of brown trout in streams is influenced by several factors and affected by the regional climate. Normally natural streams are subjected to variable climates and habitat features that may shift between season, day and even on an hourly basis. In addition, considerable differences in physical parameters such as water depth, water velocity and bottom substrate may be present within relatively short stream distances (Carlsson et al. 2004). Different physical variables are well-known to limit various fish populations, yet their relative importance may differ between streams (Heggenes 1996), and surprisingly few studies have focused on resident brown trout populations in subarctic areas (but see Saraniemi et al. 2008).

Generally the dominating data retrieval method in studies on brown trout spatial habitat selection has been electrofishing (e.g. Mäki-Petäys et al. 1999, Ayllón et al. 2009) and underwater observations (e.g. Bremset & Berg 1999, Strakosh et al. 2003). Typically, the described habitat selections of fish, by electrofishing, generate mesohabitat data while direct observations yields microhabitat data (Heggenes et al. 1999). Yet, since most of the previous studies on brown trout habitat selection have commonly been carried out on relatively small fish there is an evident need for studies on habitat selection by larger individuals.

The main objective with the present study was to investigate habitat selection of large adult brown trout during the pre-spawning period. Data on water depth, stream current and streambed substrate composition was collected and related to brown trout occurrences. Identification of preferred habitat characteristics was performed by linking habitat mapping with telemetric studies. Habitat selection was analysed with the two contrasting methods preference curves and statistical modelling. A further aim was to quantify the habitat optima for each investigated habitat variable. Finally, potential differences in habitat selection over time and between sexes were examined.

### **The biology of Brown Trout**

The review by Klemetsen et al. (2003) presented the great flexibility of brown trout in relation to environmental factors, resulting in various life-history traits. At the northern hemisphere several types of brown trout, i.e. resident and migratory, populations normally occur. In resemblance to the life-history patterns of anadromous Atlantic salmon (*Salmo salar* L.) and brown trout (e.g. Jonsson & Grawem 1985, Jonsson 1989, Rubin et al. 2004), large lakes can support migratory brown trout. These populations may employ streams for

spawning and rearing, followed by an adult phase in the lake before returning to their native stream for reproduction (Olsson & Greenberg 2004).

During their first year brown trout inhabit shallow areas (<30 cm) with moderately fast flowing water where they can maintain stationary swimming positions (Roussel & Bardonnnet 1999). Relative to age and size the fish prefer deeper and more slowly flowing parts of the stream as they grow (Jonsson 1989, Heggenes 2002). Previous studies have highlighted the complexity of freshwater communities when describing the variety of abiotic and biotic factors affecting salmonid populations (e.g. Mäki-Petäys et al. 1997, Armstrong et al. 2003). Zimmer & Power (2006) suggested that the individual fitness of stream dwelling brown trout may be influenced by a combination of numerous variables including channel geomorphology and the associated physical environment. Differential use of habitats in the wild is usually referred to as habitat selection (Armstrong et al. 2003). According to Heggenes (1996) the important physical variables influencing *in situ* habitat selection by brown trout are water depth, water velocity and current shear, substrate particle size and cover. Biotic factors can be difficult to quantify and therefore various forms of physical descriptors have generally been the subject of analyses. In nature, both physical and biological variables have an overall effect on fish habitat preferences, which consequently is dependent on complex interactions among various factors (Hirzel et. al. 2002).

## **MATERIAL & METHODS**

### **Study area**

The study was carried out in the upper reaches of River Vindelälven (65°50'N 16°30'E) at a section of about 10 km in length (Figure 1). Being located in the high boreal subarctic region of Scandinavia the studied reach is characterized by harsh seasonal changes in flows between winter and summer. The river is covered by ice from November to April. The flow at the studied section normally varies from a minimum around 8 m<sup>3</sup>s<sup>-1</sup> in late winter to 400 m<sup>3</sup>s<sup>-1</sup> in spring to early summer, with a typical autumn flow of c. 30 m<sup>3</sup>s<sup>-1</sup>. Average flow during the studied period was c. 19 m<sup>3</sup>s<sup>-1</sup>, slightly lower than normal during this time of the year (Peter Schmitt 2010 *pers. comm.*).

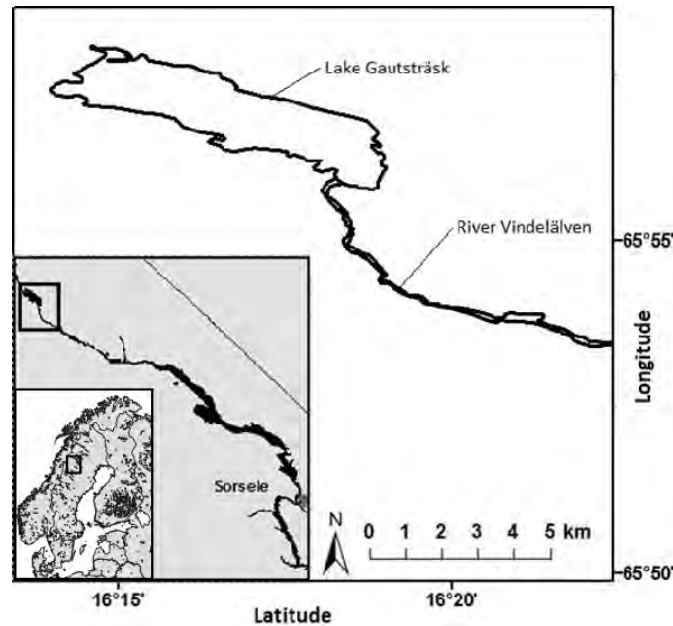


Figure 1. Map showing the study area in the upper part of River Vindelälven and the location in Sweden.

Brown trout spawning migration in the studied river part normally starts in July, attaining its maximum in August with latest spawners entering the river in the end of September. Spawning generally takes place in October-December, where after the fish may leave to both down- (Lake Storvindeln) and upriver lakes (Lake Gautsträsk), or overwinter in deep parts of the river (Rivinoja et al. 2004). Apart from brown trout, grayling (*Thymallus thymallus* L.) is common in the river. The surrounding riparian vegetation is dominated by coniferous forest consisting of Norway spruce (*Picea abies* L.) and Scots pine (*Pinus sylvestris* L.) with a mixture of deciduous trees.

### Habitat mapping

Field mapping in this study generally followed the Swedish standard method described in Molin et al. (2010). To meet the demands of data required for microhabitat modelling the whole river was visually mapped and thereafter divided into sub-sections that were thoroughly described. First, the river was separated into stretches represented by general stream characteristics, i.e. pools, riffles, rapids. Secondly, mapping of stretches was further stratified by creating separate habitat areas, also known as resource units. Again, units were defined by general features within the stretch. Thirdly, habitat descriptions from the river bank were done on each unit by observations of depth, stream current and streambed substrate. Finally, a map of the river with implemented units was constructed and measured variables were assembled.

Stream currents were classified according to composition of the velocity categories; slow flowing ( $<0.2 \text{ m s}^{-1}$ , deep and slow flowing water), slow riffle (no turbulence, smooth bottom and intermediate depths), fast riffle (turbulent water) and rapid ( $>0.7 \text{ m s}^{-1}$ , highly

turbulent water). Estimations of stream current were based on visual observations of surface flow patterns, calibrated and confirmed to velocity measurements with an Acoustic Doppler Current Profiler (ADCP, StreamPro, RDI-Teledyne). The riverbed was classified according to compositions of substrate categories; sand (0.002-2 mm), gravel (2-20 mm), stone (20-200 mm), boulder (>200 mm) and rock (>4000 mm). Depth was divided into five classes; 1 (0-0.5 m), 2 (0.5-1 m), 3 (1-1.5 m), 4 (1.5-2) and 5 (>2 m). Since several velocities and substrate compositions were found within single mapped resource units, frequencies of variables were given in proportions of the total resource unit area, following Molin et al (2010). Areas of resource units were calculated correspondingly (*average width \* average length*) using previously constructed habitat-maps and aerial photographs.

### **Fish tagging and telemetry positioning**

Within the studied river section adult brown trout were caught by sport fishing and tagged between 2 July and August 31 in 2010. A total 21 of fish fulfilled the criterion as appropriate experimental fish for tagging, thus showing good condition together with minimum stress symptom after catch. Their average total length was 70 cm (60-80 cm) and mass 4.0 kg (2.5-6.7 kg), represented by 9 females and 12 males, with sex determination based on morphological characters such as shape of body and head (i.e. hook on lower jaw). After tagging the fish were held in position in the river allowing recovery until they had regained their posture and alertness, usually lasting a few minutes.

The tracking of tagged fish was performed by using activity pulsed transmitters (ATS 2130, Advanced Telemetry System, Ohio, USA, with a mass of 28g in air and a duration of c. 2 years) operating at 151 MHz range (frequencies spaced 10 kHz apart). Manual tracking was carried out from shore (ATS R2100 and Televilt RX8910 receiver), where detailed positioning of all fish was performed at 15 occasions between 8 a.m. and 4 p.m. from 6 September to 2 October 2010 resulting in a total of 218 specific observations. Triangulation enabled positioning of fish with an accuracy of about  $\pm 5$  m. Besides this, a total of 6 antennas connected to automatic data logging receivers (LOTEK, SRX\_400) were positioned along the study section to validate fish positions, home ranges and migrational activity. Individual fish locations were plotted on the map constructed at the habitat mapping, which enabled an accurate and efficient way to evaluate habitat selection of the tagged individuals.

### **Data Analyses**

#### ***Variable reduction***

Since data was collected by the Swedish standard method the stream current and substrate cover was expressed in categories and proportions, e.g. data for substrate in a unit could be mapped as 20% stone, 50% gravel and 30% sand. In order to capture the habitat dimensions of a resource unit and with the aim to avoid ascribing habitat preferences by proportions of categories, the habitat description of a unit was expressed as an index represented by a single value. For this purpose, principal component analysis (PCA) was applied to sum up

the variation in a habitat into components. However, the derived components had a complex and non-intuitive composition of habitat variables, making interpretation difficult. As an example, the first component had high positive loadings of both high and low water velocities, implying that a resource unit could be assigned to both of these, which was not supported by the mapping, and as a consequence the PCA's were excluded. Still, there was a need to reduce the number of variables without losing too much information and the method of using habitat scores to describe composition of variables was approached.

*Creating habitat scores*

When applying this method the mapped resource units were given scores ranging between 0 and 100. The scores were calculated by multiplying proportions for every category of stream current (slow flowing, slow riffle, fast riffle and rapid) and streambed substrate (sand, gravel, stone, boulder and rock) with a given rank value (Table 1). Multiplied proportions were summed and then divided by 100 (example in Equation 1). Habitat scores represented one of each five stream characteristics and substrate compositions, generating the general features of a certain habitat score (Table 2). The grouped mesohabitat scales were selected to be comparable to others presented in the literature (e.g. Baran et al. 1997). By comparing habitat scores with the actual composition of a resource unit (see Appendix 1, Figure 1 & 2), the habitat scores were found sufficient to distinguish habitats, and consequently the scores were used in further analysis. The use of habitat scores was validated and tested against other variables (i.e. dominant, maximal and variance) in generalized linear mixed effects model (GLMM) (see Appendix 2, Table 1).

Equation 1. Example of a resource unit mapped as 70% slow flowing and 30% slow riffle, results in a habitat score of 9.99 for stream current (see Table 1).

$$Habitat\ score = ((0 \times 70) + (33.3 \times 30) + (66.6 \times 0) + (99.9 \times 0)) / 100 = 9.99$$

Table 1. Values used to calculate habitat scores for stream current and streambed substrate in mapped resource units.

Stream current	Rank Value	Substrate	Rank Value
Slow Flow	0	Sand	0
Slow Riffle	33.3	Gravel	25
Fast Riffle	66.6	Stone	50
Rapid	100	Boulder	75
		Rock	100



Table 2. Intervals for depth, stream current score and substrate score. The class names describe the general features of stream characteristics and substrate compositions within single resource units.

Class	Depth	Velocity		Substrate	
	(m)	Character	Score	Composition	Score
1	0 - 0.5	Pool	0-20	Fine	0-20
2	0.5 - 1.0	Glide	20-40	Pebble	20-40
3	1.0 - 1.5	Run	40-60	Medium	40-60
4	1.5 - 2.0	Rough	60-80	Coarse	60-80
5	>2.0	Shoot	80-100	Large	80-100

## Preference curves

Preference curves, also known as suitability curves, describe habitat selection of a species through analysis of habitat use and availability. The use may be termed selective when resources are utilised disproportionately to their availability. Here, the development of univariate preference curves generally followed the methods of Baltz (1990). Each variable was divided into five classes based on intervals of habitat scores (Table 2). Histograms of proportional availability and frequency-of-use were constructed for the five classes of depth, velocity and substrate compositions. By calculating the relative frequency of use of each increment it was possible to compute the proportional use for each class based on habitat availability according to Equation 2 (standardised to values from 0 to 1). Univariate depth, velocity and substrate class preference curves were developed independently by fitting polynomial regression functions of 3<sup>rd</sup> and 4<sup>th</sup> order to preference data (results in Figure 2a, b and c).

Equation 2. Used to derive  $E$  = index of electivity, by using forage ratio where:

$$E = \frac{U}{A} = \frac{\text{proportional use of resource class } i}{\text{proportional availability of resource class } i}$$

## Statistical modelling

### *Data exploration*

Correlation between explanatory variables was investigated by pairplots. As these correlations were found to be low the linearity between response variables and explanatory variables was assessed by incorporating a LOESS smoother into the pairplot (Appendix 2, Figure 1). Cleveland plots were also used to assess homogeneity of variance in the raw data, where no heteroscedastisty could be detected, further illustrating how the mapped data was categorised, by producing variables sets that were not completely continuous (Appendix 2, Figure 2).

### ***Analytical progression***

The data was modeled according to three main questions (see below). The analytical progression is presented for all questions, however statistical inference will only be concluded based on the final model used.

#### *1. Do the trout have a specific preference of depth, water velocity and substrate?*

A hypothetical data-set where trout were spread across available habitats (i.e. not having any particular preferences) was created by randomly assigning 10 habitat observations for every true individual observation. This generated a presence-absence dataset where the presence data corresponded to the true observations (i.e. the resource unit where the fish was observed) and the absence data corresponded to the 10 randomly selected observations (i.e. 10 randomly selected resource units out of the 71 units available). Since inspection of the pair plot with integrated LOESS smoothers (Appendix 2, figure 1) indicated non-linearity between the response variable and the explanatory habitat variables the use of general linear models (GLM) was discarded and data was approached with generalized additive models (library “mcgv”) with binomial errors. To account for pseudo replication due to repeated measures on individuals, a generalized additive mixed model (GAMM, library “mcgv”) with binomial errors was fitted to the data. The presence-absence data was used as the binary response, velocity and substrate as smothered (splines) continuous explanatory variables, and depth as a five-level nominal variable. Individual was added as a random effect. Plotting of GAMM model indicated a lack of observations in some of the resource units, i.e. for habitat scores between 0 and 50 (see Appendix 2, figure 3). Hence, the original GAMM plot for substrate (Appendix 2, figure 3) was cut to account for the limited amount of observations for certain habitat scores. Degree of smoothing (number of splines) was evaluated through cross-validation, using Akaike information criteria (AIC) (see Appendix 2, table 2). Only main-effects were considered, and no factorial models were evaluated due to convergence problems in the used software R.

#### *2. Is there any difference in habitat choice between sexes?*

Inspection of the pairplot (Appendix 2, figure 1) suggested a linear relationship between response variable sex and the explanatory variables velocity and substrate. This was also confirmed by GAMM plots (using sex as a binary response) (Appendix 2, figure 4). Hence, parametric models were used to estimate the probabilities of finding a specific sex as a function of depth, velocity and substrate in a generalized linear model with binomial errors (logistic regression). Relevance of habitat variables were evaluated by model comparisons and significant increase in deviance of a reduced model was assessed by chi-squared tests (Table 3). Non-significant interaction terms were removed in accordance to the principle of Parsimony, where a reduced model is preferred to a more complex model (Crawley 2007). To compare a model with and without correction for pseudoreplication, a generalized linear mixed model (GLMM, library “lme4”) with binomial errors was also fitted to the data, keeping the same fixed effect structure as the GLM, but adding individual as a random effect. Treating individual as a random effect accounts for dependence of observations within individuals.

### *3. Is there a trend in habitat use over time?*

Inspection of the pair plots with incorporated LOESS smoothers indicated linearity between the response variables velocity and substrate and the explanatory variable day (Appendix 2, figure 1). Presence of a trend over time in habitat use of velocity and substrate, was initially analyzed with general additive models (GAMM) using day (time elapsed) as a smothered continuous explanatory variable and velocity and substrate as response variables (Appendix 2, figure 5). Two models, one for velocity and one for substrate were fitted. Degree of smoothing was evaluated through cross-validation using AIC as selection criteria (Appendix 2, table 4). GAMM models suggested a linear relationship in both models. A parametric approach was hence considered. Velocity and substrate was log transformed and modeled as a function of day using linear mixed models (LMM, library “nlme”), treating individual as a random effect. Log transformation enabled response variables to be treated as normally distributed and hence enabled the use of less advanced modeling.

## **RESULTS**

### **Preference curves**

According to the observed distribution of fish, their habitat use differed statistically from a random predicted distribution (Chi-square test,  $\chi^2 = 101.4$ , d.f. = 4,  $P < 0.01$ ), demonstrating a selective use of the sampled units. The overall preferred depth was 1-2 m while shallow areas 0-0.5 m deep, typically located closer to the river banks, was used proportionally little (Figure 2a). In general the fish favoured slow riffle habitats ( $0.2-0.4 \text{ m s}^{-1}$ ) linked to slow flowing ( $<0.2 \text{ m s}^{-1}$ ) and fast riffle areas ( $0.4-0.7 \text{ m s}^{-1}$ ) characterised as pools and glides (Figure 2b). A selection of glides indicates a preference for habitats with a large element of slow riffle and small element of fast riffle. Fish used runs in the expected proportion while pools were used moderately (Figure 2b). Trout favoured sites with fine ( $0.02-2 \text{ mm}$ ) and large ( $>200 \text{ mm}$ ) substrates, represented by score intervals 0-20 and 80-100 (Table 2, figure 2c). Data displays a low fish preference for the intermediate composition, despite its high availability (Figure 2c).

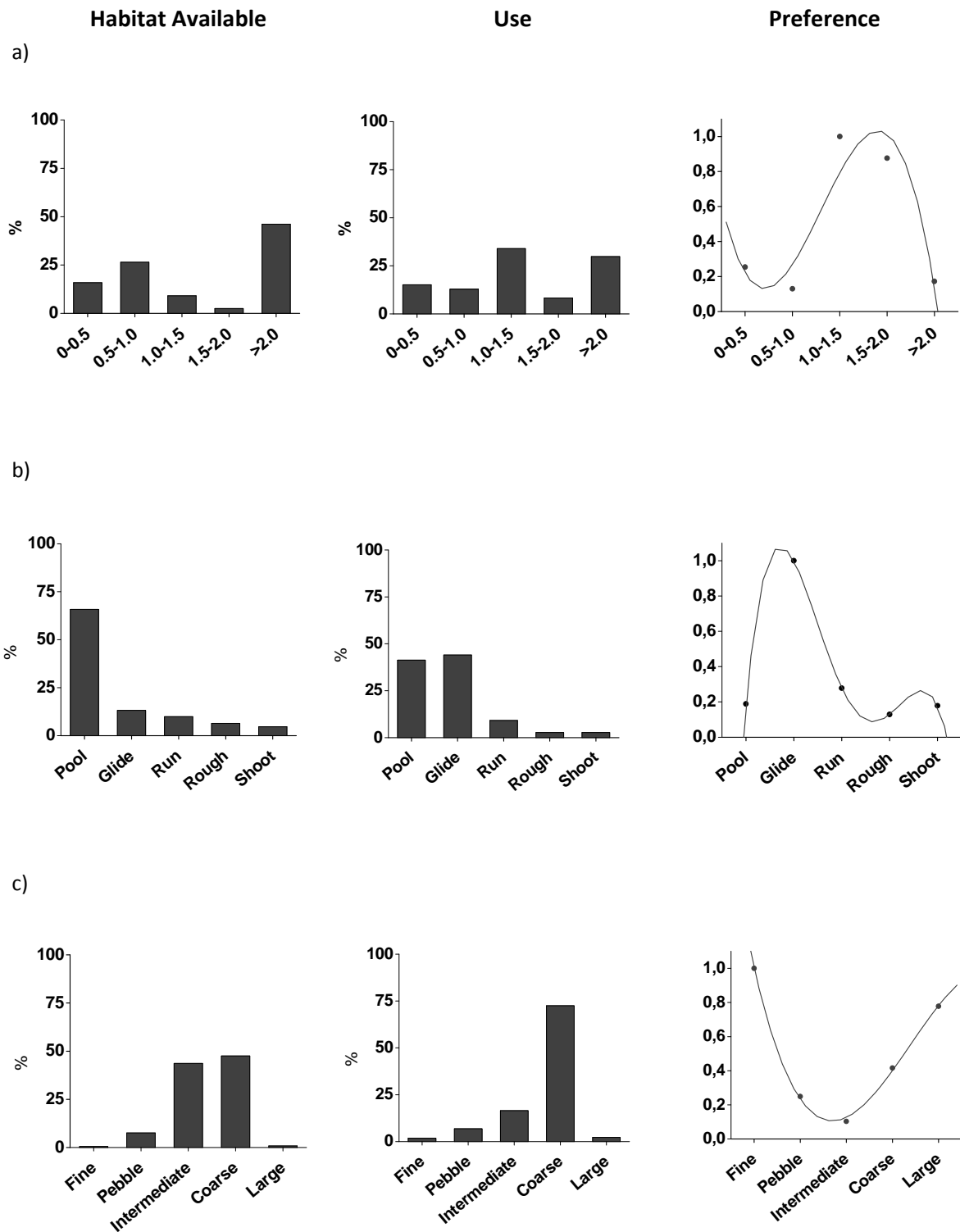


Figure 2. Availability, use and preference of (a) depth, (b) velocity and (c) substrate. Depth curve (P.I. =  $-0.1312d^3 + 1.0266d^2 - 2.114d + 1.4379$ ;  $R^2 = 0.8814$ ). Stream velocity curve (P.I. =  $-0.1034v^4 + 1.3846v^3 - 6.4906v^2 + 12.142v - 6.744$ ;  $R^2 = 1$ ). Streambed substrate curve (P.I. =  $-0.0463x^3 + 0.6083x^2 - 2.2705x + 2.7123$ ;  $R^2 = 0.9982$ ).

## Statistical modelling

### 1. Do the trout have a specific preference of depth, water velocity and substrate?

The general additive mixed effects model (GAMM) indicated that all the investigated habitat variables had a strong statistical influence on trout habitat selection ( $p < 0.001$ ). Hence, depth, water velocity and substrate influenced the probability of trout presence as compared to a random distribution. Since higher degrees of freedom resulted in lower AIC, thus inferring complexity, cross validation further reinforced the presence of non-linearity among the variables velocity and substrate. Based on AIC, the default degree of smoothing in GAMM model 1 was the most appropriate to use for these variables (Appendix 2, table 2). Plotting of the final GAMM models displayed a complex non-linear relationship for both velocity and substrate habitat scores (Figure 3, 4). GAMM plots illustrate the probability of finding a trout (Y) as a function of velocity habitat score (velscore) or substrate habitat score (subscore) (X). As illustrated by Figure 3, there is an almost equal probability of finding a trout in habitats with velscores of 10, 38 and 65, while the plot indicates a low probability of finding trout in habitats with velscores of 20, 50 and  $>75$ . This infers that trout is more likely expected to be found in pool, glide and run (c.  $0.2-0.7 \text{ m s}^{-1}$ ), than in rough and shoot ( $>0.7 \text{ m s}^{-1}$ ) velocity characters (Table 2). The probability of finding a trout is high in habitats with subscores of 63 and 75, signifying that trout selected habitats with coarse ( $>200 \text{ mm}$ ) bottoms before fine, pebble and medium ( $0.002-200 \text{ mm}$ ) substrate compositions (Table 2, figure 4). Yet, the GAMM plot show relatively wide confidence intervals (Figure 4), indicating imprecision in the estimates.

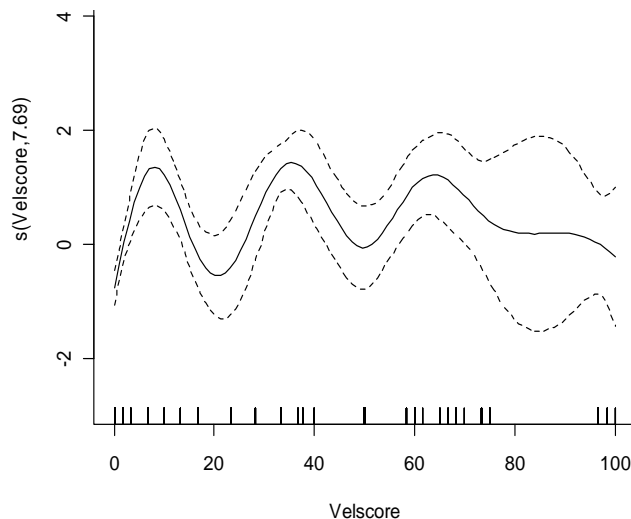


Figure 3. Final GAMM model plot for velocity (solid line) and confidence intervals (dashed lines).

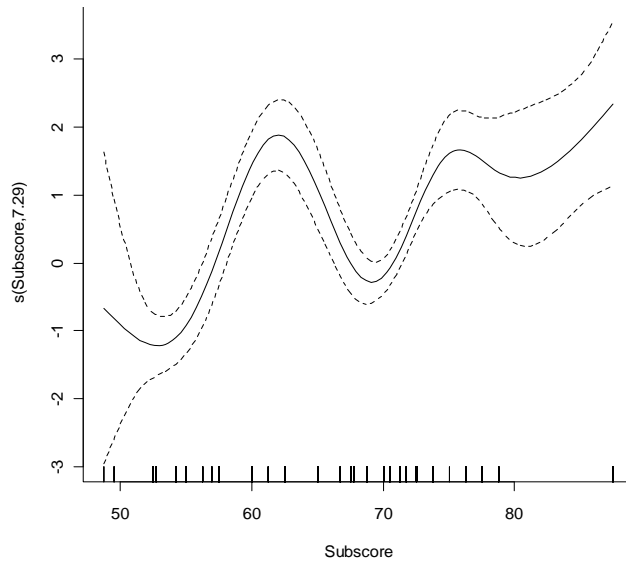


Figure 4. Final GAMM model plot for substrate (solid line) and confidence intervals (dashed lines).

### 2. *Is there any difference in habitat selection between sexes?*

The result of a small and insignificant change in deviance from the maximal model when removing variables depth and substrate (subscore) indicated low effect of these variables on sex. According to model selection water velocity (velscore) was the only variable significantly differentiating the sexes habitat selection (Table 3), where males used higher velocities than females. However, the more advanced mixed model (GLMM) did not demonstrate any differences between the sexes in relation to the studied variables (Appendix 2, table 3).

Table 3. Model selection by using deviance from maximal model and variable reduction according to principle of Parsimony (Crawley 2007). Maximal model ( $\text{glm}(\text{SexBin} \sim \text{Velscore} + \text{Subscore} + \text{Depth}, \text{data} = \text{Real}, \text{family} = \text{binomial})$ ).

GLMM model	Deviance	P(> Chi )
- Depth	-0.77389	0.379
- Depth+Subscore	-0.9631	0.3264
- Velscore	-232.3	<0.001

### 3. *Is there a trend in habitat selection over time?*

The linear mixed effects model (LMM) was non-significant in describing brown trout habitat use over time (Table 4). As a consequence this notifies that the influence of velocity and substrate use on the fish over the study period could not be evaluated by this method.

Table 4. Results from linear mixed effects model where water velocity (velscore) and substrate composition (subscore) was modeled as a function of day.

LMM model	Variable	Std. Error	d.f.	t-value	P
Velscore ~Day	Day	0.279452	200	-0.272512	0.7855
Subscore~Day	Day	0.1646631	200	0.424534	0.6716

## DISCUSSION

Evidently brown trout have a specific preference for certain habitats as demonstrated here by the non-random distributions regarding water depth, velocity and substrate compositions. The results from this study, where large brown trout in a subarctic region was examined may be difficult to contrast to other studies that usually have focused on smaller fish in smaller rivers in more southern areas. At the same time there seem to be a variety of techniques used in different studies to evaluate habitat preferences of brown trout, which complicate direct comparison between studies. In the section below; general habitat preferences of the fish found in this study is related to findings by others, while the use of various evaluation methods is discussed. Finally issues regarding fisheries management of brown trout in rivers are highlighted.

### Habitat selection

This study demonstrated that habitat selection for large brown trout during the pre-spawning period was significantly influenced by water depth, stream velocity and riverbed substratum. In general the studied brown trout seemed to exploit a larger variety of used velocities, ranging from low to intermediate speed, than substrates that was dominated by coarse fractions (relationships displayed by the GAMM curves). In contrast, Greenberg et al. (2001) found that brown trout favored pools while no significant preference of substrate was found. During the study period in the present work (26 days) no significant trends in habitat utilisation over time could be detected. However, Saraniemi et al. (2008) studied trout over a year and found a high variation in habitat use, attributed to upstream, spawning, overwintering and downstream migrations. Movement and behaviour in fish has been linked to environmental variables where water temperature appears to be a critical determinant of habitat selection (Zimmer et al. 2010). Although, no measurements of water temperature were taken in this study, these variations are expected to be relatively low and not cause any particular trend in habitat use over the study period.

### *Depth preference*

The brown trout in this study showed a high preference of depths from 1 to 2 m. These areas most likely represent adequate secure holding areas. Yet, habitats with depths > 2 m seemed to be unexploited, possibly because of their low water velocities and the fact that fish were close to their spawning period. Dieterman et al. (2006) found a positive

correlation between presence of large brown trout and depths  $> 0.9$  m, however, they were not able to evaluate fish preferences for deeper waters, likely because of the rarity of these depths in their study. In contrast to Strakosh et al. (2003), who found that trout preferred depths of c. 0.6-1.1 m, the fish in this study preferred deeper water. These differences might be explained by the smaller size of fish in their work, which therefore may indicate that larger fish prefer deeper areas. The observations from this study consequently support the previous ones, declaring the bigger fish/deeper habitat relationships (Schlosser 1987, Mäki-Petäys et al. 1997). Another explanation to the differentiation in depth use between studies might be dissimilarities between the study streams and others have demonstrated that brown trout tend to use deeper and lower velocity areas in larger rivers than in small streams (e.g. Louhi et al. 2008). As declared by Heggenes (2002), the use of depth by brown trout can show a large variation depending on stream characteristics where water transparency also appears to be an important determinant in the vertical distribution of brown trout (Klemetsen et al. 2003). This could influence the present results as the water in the studied stream is particularly clear, hence, the fish in this study may prefer deeper waters than they would in humid rivers of same size. In addition, competition of preferred deep river parts can result in space restrictions for large trout if suitable water depths are limited (Heggenes et al. 1999). Conclusively, the deeper water preferences of fish in this study, as compared to previous ones, may be explained by the fact that most of the other studies have focused on smaller fish. No difference in depth preferences between sexes could be established, and according to the GLM model both sexes utilized the available depths equally, also supported by the more complex GLMM model.

### ***Velocity preference***

As found here the brown trout generally preferred stream characteristics represented by slow riffle habitats ( $0.2-0.4 \text{ m s}^{-1}$ ) linked to slow flowing ( $<0.2 \text{ m s}^{-1}$ ) and fast riffle areas ( $0.4-0.7 \text{ m s}^{-1}$ ). These areas of pools and glides have also been found as preferable for brown trout by others (e.g. Heggenes 1996, Heggenes et al. 1999, Burrell et al. 2000, Vismara et al. 2001, Saraniemi et al. 2008). According to Hendry et al. (2003), the general velocity requirements of salmonids would normally be present in riffle/pool sequences in high gradient areas, and riffle/glide/pool sequences in low gradient areas. Bunnell et al. (1998) found that although pools were used most often, runs and riffles also contribute to fish survival. The preferences of stream current found on brown trout in this study generally harmonised with previous findings, where divergences may however be expected dependent of fish size.

The differences, found here on preferred stream velocities, between females and males (where males used areas with significantly higher velocities) support the theory of sexual dimorphism in habitat use. This detail was also identified in the review by Klemetsen et al. (2003), which notify that brown trout males tend to exploit running waters while females are more inclined to pelagic waters. Others have indicated that growth rate of trout in pools may be better than in riffles (Greenberg & Giller 2001) and that there seems to be a close connection between sex, growth rates and habitat selection of brown trout (Jonsson 1989).



### ***Substrate preference***

The results from the preference curves showed that brown trout selected large and fine substrate compositions such as boulder (>200 mm) and sand (0.02-2 mm) areas. No difference in preferences between sexes could be established and overall the intermediate substrate compositions were not widely used. Comparable results on substrate preference of brown trout have been demonstrated by others (e.g. Greenberg et al. 1996, Bergengren & Thyrel 1997, Vismara et al. 2001 and Teixeira & Cortes 2007). Vismara et al. (2001) suggested that habitat selection might be influenced by the substrate heterogeneity, where a low heterogeneity may result in a narrow use of coarse substrates. Parallel conclusions can be drawn from this study area in River Vindelälven, which also displays relatively low substrate heterogeneity. Although, trout here generally preferred stony bottoms they were also found at fine grained substratum like sand, gravel and silt, results matching with the findings by Heggenes et al. (1999). The selective use of fine and large substrates might be explained by diel patterns in activity and feeding regimes, as stated in the study by Vismara et al. (2001). Coarser substrate has also shown to provide lower water velocities close to the bottom creating microhabitat space for resting (Heggenes 1996). The overall preference might be influenced by the available substrate types in the examined rivers. However, as demonstrated in this study the high proportion of intermediate substrates were hardly used by the brown trout, suggesting that the prevailing substrate type do not necessarily affect their habitat selection. No difference in substrate preferences between sexes could be established, and according to the GLM model both sexes utilize coarse bottom substrates, also supported by the more advanced GLMM model.

### **Consideration of evaluation methods**

A correlation between fish abundance and specific habitats imply a possibility to do predictions on the relationships between habitat use and habitat features. Yet, selection or avoidance of a particular resource is not directly revealed by the predicted use (Rabeni & Sowa 1996) that may be difficult to describe (Rosenfeld 2003). Nevertheless, information of resource preferences gives important details usable for various evaluations (Manly et al. 2002). At the same time, the dynamics of fish-habitat relationships is undoubtedly complex, and as stated by Armstrong et al. (2003) various models should only be regarded as simplifications of multiple ecological processes. Habitat-use models accounting for a majority of the abiotic and biotic factors would be satisfactory, however, logistically problematic.

There are several difficulties in interpretation when comparing the result from this study to previous ones on habitat preferences of brown trout. First, there is a lack of standardization for measurement and classification of depth, velocity and substrate. Secondly, a lack of standardization in the definition of fish size, where some authors use age and others use length or in some cases both. The final difficulty is the fact that depth and velocity tend to be correlated hence leading to problems in separating the effect of these two variables. Since water velocity tends to be less and depth greater in pools than in riffles there is a tendency for negative correlation between depth and velocity (Crisp 2000). Incorporating

rare habitats also induces some difficulties when creating preference curves as classes with low representation degree may create unstable indexes (Krebs 1999).

### ***Preference curves***

The present study has identified some of the difficulties with using habitat preference indexes. The most familiar index of selection, in respect to habitat preference criteria, has been the forage ratio commonly used in the instream flow incremental methods (IFIM), presented by Bovee et al. (1998) and Baltz (1990). The standardized preference indexes defines the likelihood that a given resource type will be selected when offered on an equal basis with resource types (Manly et al. 2002). Knowledge of the degree to which preference curves accurately reflect habitat quality and their biological relevance is fairly poor and true fitness consequences are required to achieve realistic predictions (Rosenfeld 2003). In addition, when comparing habitat use by radio-tagged fish in this study with other data, one must keep in mind the importance of various stream characteristics and the limitations of each survey method.

### ***Statistical modelling***

Modern analytical methods, such as the modelling done in this study, can be capable alternatives to preference indexes. By formulating habitat preference as a function of possible explanatory variables one is able to evaluate not only the statistical significance of a variable, but also to test complex hypotheses such as interaction between variables. It is noteworthy that some of the conclusions obtained from the preference curves differed rather substantially from those obtained from statistical modelling. Caution should however be taken when interpreting some of the modelled habitat scores. In the majority of resource units categories of habitat variables were adjacent to each other, creating a distinct relationship between score and composition of substrate or stream velocity. Although in few cases, a resource unit was composed of variable categories that were not adjacent (e.g. sand and rock), generating bimodal curves. In such instances, habitat scores gives an inaccurate characterisation of the resource unit as a false intermediate score referring to a composition of intermediate substrate or current type would be derived (see Appendix 1, Figure 1 & 2, bimodal distribution of mesohabitats - i.e. resource unit 5.2, figure 1). However, previous scenarios were rare and did not pose a problem for the analysis in this study.

### ***Aspects of using Swedish standard habitat mapping method***

Using the Swedish standard method of habitat mapping to collect habitat data induces both positive and negative aspects regarding data quality. The mapping method creates a complex set of data, comprising both categorical and frequency data, which may be problematic to analyse. The positive property of a complex data set is that it gives us the opportunity to reflect some of the complexity in natural stream environments. According to Rosenfeld (2003) predictions of fish density is often more accurate when using discrete habitat classes rather than continuous measurements. This supports the use of observational studies like the Swedish mapping method, which may characterize habitats in a more biologically meaningful way than continuous measurements.

## **Management implications**

Salmonid populations can be highly variable over time displaying abundant life history features, which may also lead to flexible habitat selections (Milner et al. 2003). This variability might cause difficulties for fisheries managers since it introduces uncertainties, and there is often a lack of information on vital aspects like overwintering habitat, migratory patterns, spawning and rearing habitat. The population examined in this study exhibits migratory patterns between downstream or upstream located lakes, however their spawning migration pattern is not yet fully understood, which may complicate future management strategies.

The observed "bigger fish/deeper habitat" relationships found in this study, also supported by others (e.g. Schlosser 1987, Mäki-Petäys et al. 1997), indicates that river rehabilitation resulting in deeper water, lower water velocities and larger substrata may be rewarding for the brown trout in the river. Thus, river rehabilitation may enhance some of the important identified river characteristics preferred by large brown trout, as verified in other studies (e.g. Vehanen et al. 2010). Improving physical conditions of streams by creating habitats with suitable depths, currents and substrates may ultimately lead to an increase of salmonid populations (Greenberg et al. 2001).

## **CONCLUSIONS**

The natural process of brown trout habitat selection is complex and influenced by several factors. When comparing studies of habitat selection one must consider the size of the studied aquatic system, which may cause various habitat optima for organisms dependent on habitat availability. Habitat selection is also influenced by the size of fish due to behavioural differences between small and large fish. Although preference indexes provide a mean to assess relative preference of habitat, they do not allow for statistical evaluation of the importance of variables on preference. Several difficulties were noted in this study when comparing the results to previous studies. This indicates a big influence on the methods used when analyzing habitat preference and one should be cautious when interpreting results from indices. There is also a need to standardize the methods used to investigate habitat selection in order to reduce inconsistency between studies. We are not able to explain all or even most of the variation in natural environments. However, statistical modelling and indexes provides us with a starting point in the line of acquiring a subset of critical habitat features. The challenge for the future lies in the development of models accounting for a wider range of abiotic and biotic factors. This will in turn be a step towards better understanding of the brown trout ecology, allowing us to develop the scientific output into management implications, leading to improved sustainable use of our natural resources.

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## APPENDIX 1

### *Reducing the initial maximal model*

An initial maximal model was fitted to the data and several computed variables were tested in a generalized linear mixed effects model (GLMM). According to AIC, habitat scores were significantly more appropriate to use than dominating substrate or current, variance and maximal value of substrate or velocity (Appendix 1, table 1). The model was reassessed and non-significant interaction terms were removed in accordance to the principle of Parsimony (Crawley 2007). Individuals were assigned as a random variable, allowing for individual variation along the intercept.

Table 1. Aikake's information criterion (AIC) and degrees of freedom (df) for computed variables in the maximal generalized linear mixed effects model (GLMM).

	d.f.	AIC
Habitat score	5	1434.803
Dominant	5	1463.358
Variance	5	1461.177
Max	5	1467.147

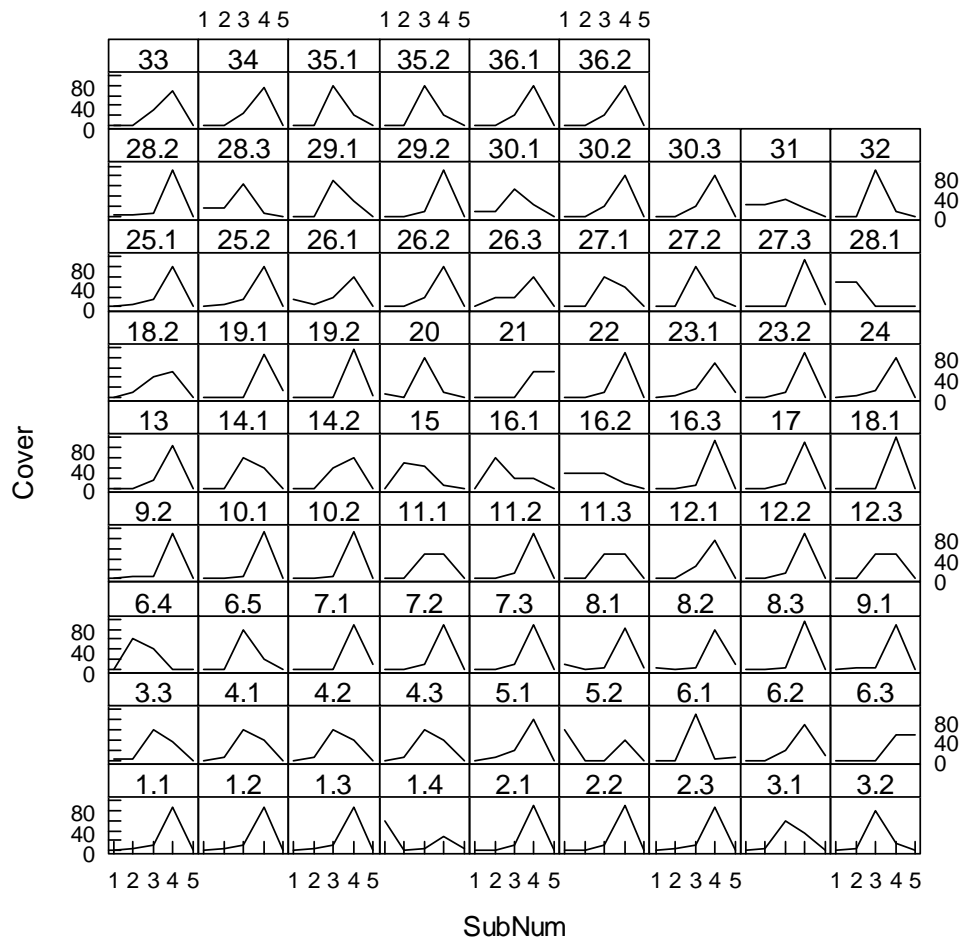


Figure 1. All mapped resource units and their cover of substrate scores.

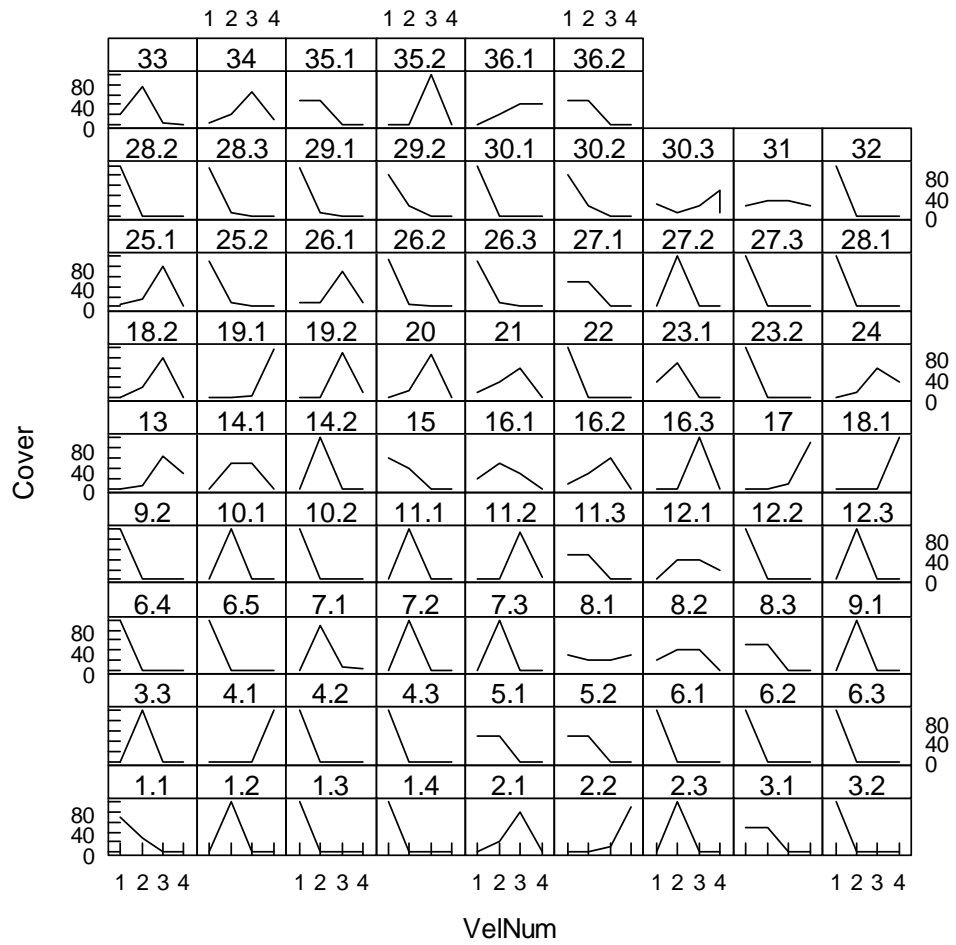


Figure 2. All mapped resource units and their cover of velocity scores.



## APPENDIX 2

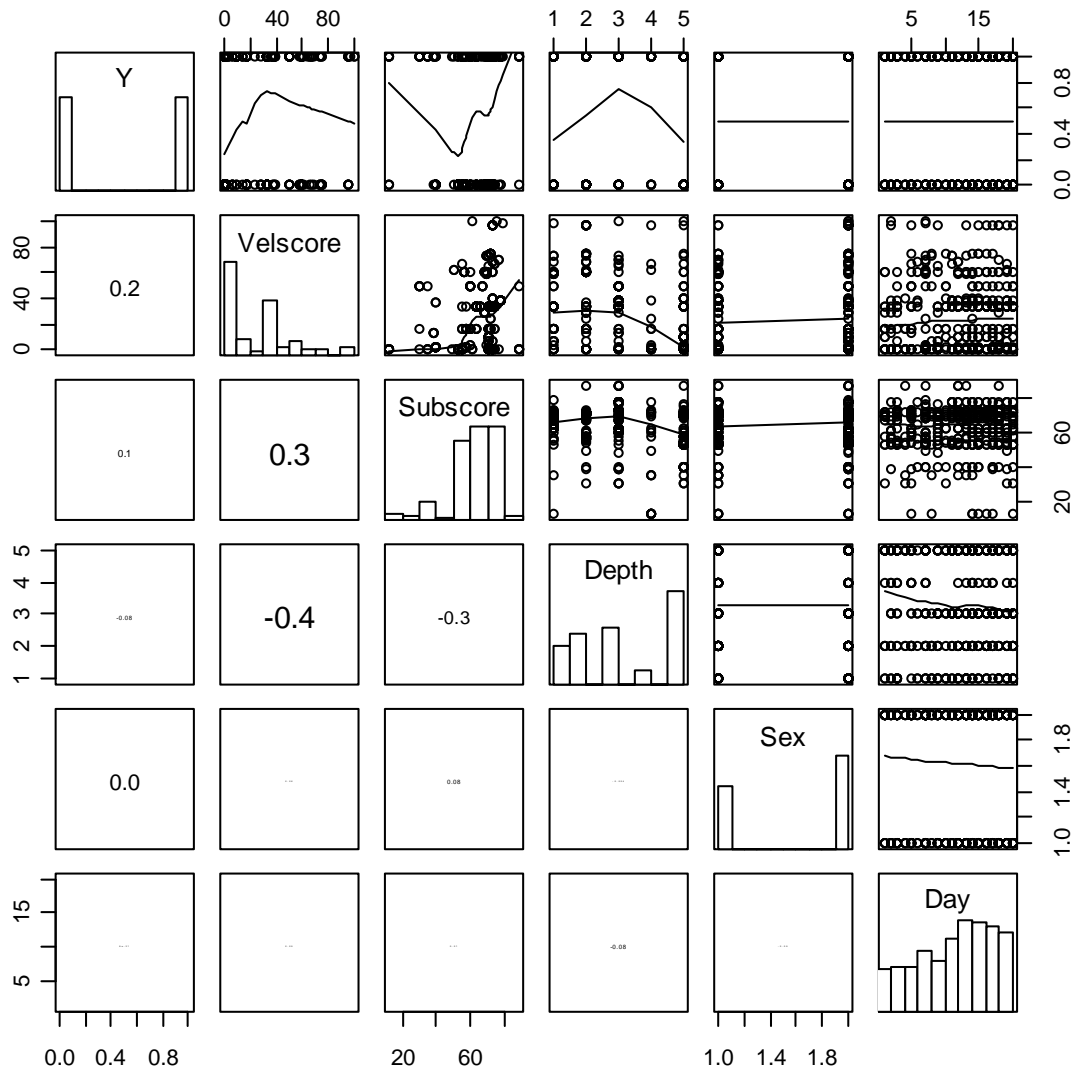


Figure 1. Pair plot to test for correlation in between explanatory variables and response variables.

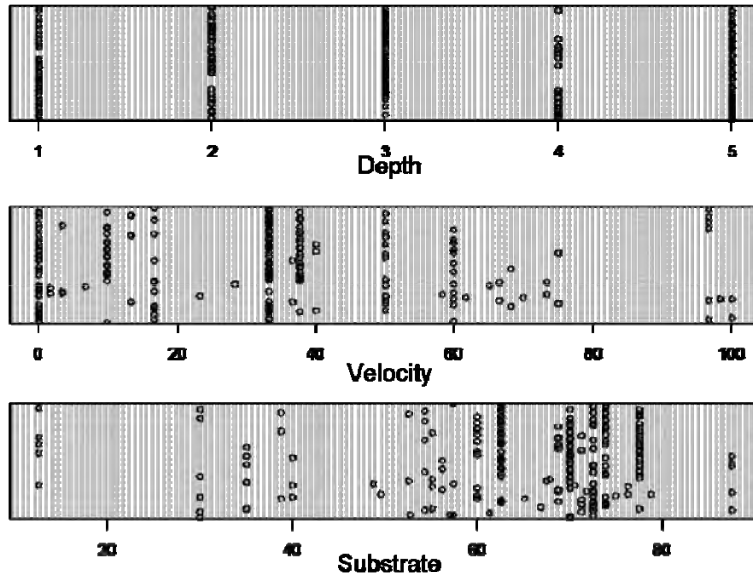


Figure 2. Cleavland dotplots.

Table 1. Test to see if more randomizations increase explanatory power of available habitat.

Randomizations	Random mean subscore	Real mean subscore
1	61.08601	64.56881
3	60.92775	64.56881
5	60.86651	64.56881
7	61.0059	64.56881
10	60.99564	64.56881

Table 2. Cross validation to test degree of smoothing in GAMM models developed for question 2 using AIC criterion.

	GAMM model	d.f.	AIC
Velocity	1	9.42752	1310.45
	2	6	1362.023
	3	3	1385.425
Substrate	1	9.40199	1310.138
	2	6	1382.382
	3	3	1394.380

Table 3. Summary of general linear mixed effects model (GLMM).

	Estimate	Std. Error	z value	Pr(> z )
(Intercept)	13.960650	48.151683	0.290	0.772
Velscore	0.009059	0.361383	0.025	0.980
Subscore	0.004980	0.533860	0.009	0.993
Depth	0.049434	5.644623	0.009	0.993

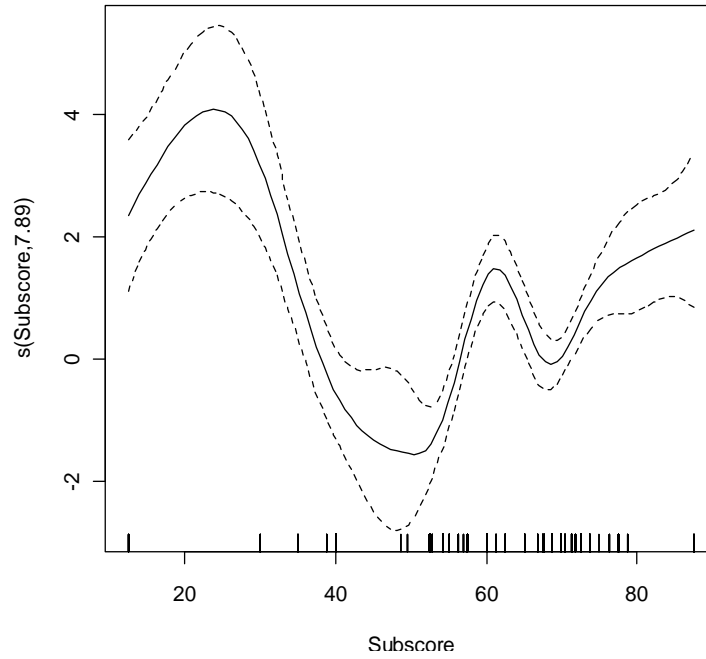


Figure 3. Original GAM plot for substrate.

Table 4. Cross validation to test degree of smoothing in GAMM models developed for question 3 using AIC criterion.

	GAMM model	d.f.	AIC
Velocity	1	3	2018.852
	2	5	2020.299
	3	11	2025.480
Substrate	1	3	1778.856
	2	5	1781.655
	3	11	1787.342

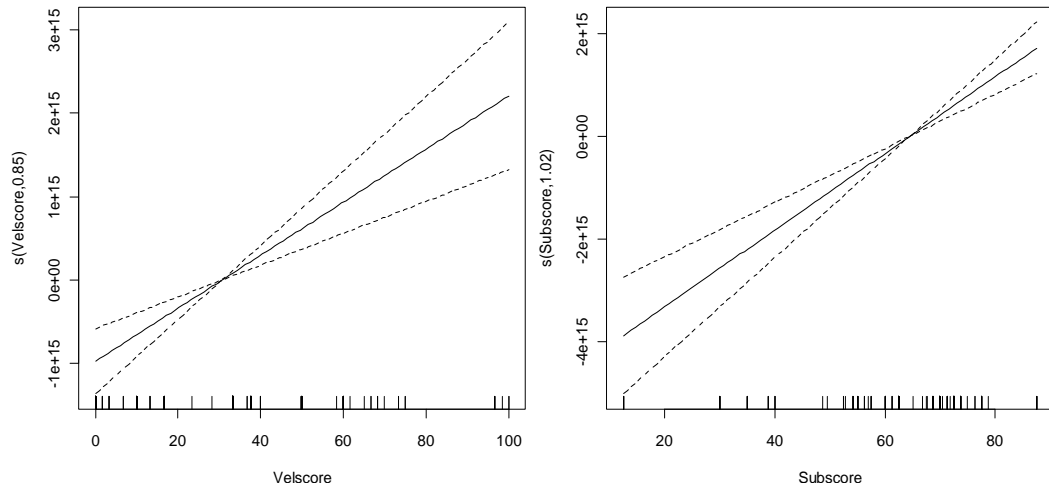


Figure 4. GAMM plot for velocity (left) and substrate (right) using sex as a binary response.

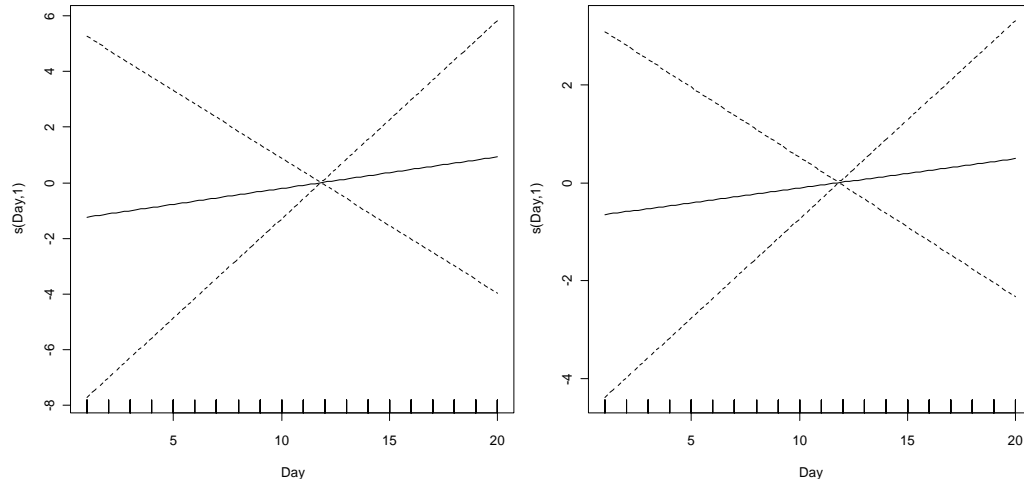


Figure 5. GAMM plot displaying trend in habitat use of velocity (left) and substrate (right) over time.

## SENASTE UTGIVNA NUMMER

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