Relationships between juvenile brown trout (*Salmo trutta*) densities, their in-stream habitat, and riparian and watershed characteristics in tributary streams of the Numedalslågen River, Norway

Sammenhenger mellom tettheter av ørretunger (*Salmo trutta*), elvehabitat og forhold i kantsoner og nedbørsfelt i sidevassdrag til Numedalslågen

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Preface

Why are there more fish in some streams and some stream sections than elsewhere? What determines this pattern? The answer is pretty easy: everything. The trickier part is identifying which factors are more influential. Model selection is the art of approximation, and given that we cannot understand patterns of infinite complexity with only finite samples, we must employ Occam' razor to "shave away all that is unnecessary".

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Contents

Abstract

I used a two-stage information-theoretic modeling approach to relate the densities of juvenile brown trout (*Salmo trutta*) in 12 second to fourth order tributary streams of the lower Numedalslågen River, Norway, to their physical surroundings at three spatial scales. Juvenile brown trout in pool habitats were counted from the stream bank at a median of five 25 m sections in each stream during summer low-flow conditions in July/August 2005. I recorded physical habitat features at the in-stream scale and land cover and land use at the reach buffer scale on site, whereas watershed-scale data on topography, surficial geology, land cover, and land use were extracted from existing databases using GIS. The best approximating models of mean juvenile brown trout density at the watershed scale included a positive relationship with stream gradient and proportion of moraine in the watershed, and a negative relationship with the proportion of bedrock. The best approximating models of density variation at the reach buffer scale included interaction models of variability of riparian width in relation to the proportion of the buffer which was either logged or under agricultural land use. A quadratic function of depth was the single best approximating model at the in-stream scale, predicting higher densities than expected for the entire stream in 25 – 44 cm deep pools. The best watershed-scale models received greater absolute support ($0.63 < R^2 < 0.72$) than did the models at the two smaller spatial scales ($0.05 < R^2 < 0.18$; reach buffer, $R^2 = 0.31$; in-stream). My findings provide a quantitative means for understanding the variation in juvenile brown trout abundance among streams and within streams and suggest that there exist multiple controlling factors over juvenile brown trout abundance across multiple spatial scales in these tributary streams. The watershed-scale factors identified in this study were most likely influencing the geomorphology of stream channels, whereas the reach-buffer factors set the stage for in-stream habitat structure by sediment-related mechanisms, primary production, and formation of pool habitats, in which depth proved to be the most influential over juvenile density. Managers should examine watershed-wide constraints of fish production before considering fine-scale management actions. Multiscale studies bridge the spatial gap between fisheries research and management and, when embedded in an information-theoretic modeling approach, are more likely to increase our knowledge of stream salmonids.

Sammendrag

Jeg undersøkte sammenhenger mellom tettheten av ørretunger (*Salmo trutta*) i 12 andre- til fjerdeordens sidebekker til de nedre delene av Numedalslågen og omgivelsene deres på tre forskjellige romlige skalaer ved hjelp av en tostegs informasjonsteoretisk modelleringsmetode. Jeg gjorde tellinger av ørretunger i kulphabitat fra elvekanten ved lav vannføring i juli og august 2005 i fem seksjoner à 25 m i hver elv. Jeg undersøkte fysisk habitat i elva og vegetasjonsdekke og arealbruk i kantsonen av elva etter fisketellingene. Data for topografi, løsmassegeologi, vegetasjonsdekke og arealbruk i nedbørsfeltene ble hentet fra eksisterende databaser ved hjelp av GIS. En positiv sammenheng med gradienten til elva og andelen morene i nedbørsfeltet, og en negativ sammenheng med andelen grunnfjell i nedbørsfeltet, beskrev mønsteret i gjennomsnittstetthet av ørretunger i elvene best. I kantsonen beskrev interaksjonsmodeller mellom variasjonen i kantsonebredde og andelen av kantsonen som var enten hogd skog eller omgjort til åker variasjonen i tetthet av ørretunger best. En andregradsfunksjon av kulpdybde var den beste modellen for habitat i elva, og predikerte større tetthet enn det som var forventet tetthet for hele elva i kulper som var 25 – 44 cm dype. De beste modellene på nedbørsfeltnivå forklarte en større andel av variasjonen i data ($0,63 < R^2 < 0,72$) enn de beste kantsonemodellene ($0,05 < R^2 < 0,18$) og den beste habitatmodellen ($R^2 = 0,31$). Disse funnene gir en kvantitativ bakgrunn for å forstå variasjonen i tettheten av ørretunger mellom vassdrag og innenfor vassdrag, noe som kan bety at det finnes mange faktorer på flere romlige skalaer som kontrollerer tettheten av ørretunger i disse sideelvene. Nedbørsfeltfaktorene påvirket sannsynligvis geomorfologien til elvene, mens kantsonefaktorene dannet grunnlaget for habitatstruktur i elva gjennom sedimentrelaterte mekanismer, primærproduksjon og dannelse av kulphabitat, der dybde viste seg å være den viktigste habitatfaktoren. Forvaltningen bør undersøke begrensninger av fiskeproduksjon på nivå av nedbørsfelt før man vurderer finskala tiltak. Flerskalaundersøkelser gjør noe med spriket mellom fiskeribiologiske undersøkelser og forvaltningsutfordringer, og bidrar til økt kunnskap om laksefisk i elver særlig når de kombineres med informasjonsteoretisk modellering.

Introduction

Anadromous salmonids in the genera *Salmo* and *Oncorhynchus* are facing rapid population declines and even extinction (Parrish *et al.* 1998). There are several factors that are likely contributing to the declines, such as over-harvesting, reduced post-smolt survival, genetic deterioration by interference with farmed fish, changing climate, and deterioration of freshwater spawning and rearing habitats (Nehlsen *et al.* 1991, Bradford & Irvine 2000, McGinnity *et al.* 2003). Central to the uncertainty regarding the magnitude of the negative effects acting on the stocks is that fisheries ecologists have conducted research primarily at small spatial scales, which has made it difficult to untangle the relative importance of various factors as well as initiate constructive management actions (Lewis *et al.* 1996, Wiley *et al.* 1997, Fausch *et al.* 2002).

Although anadromous life cycles are complex and the individuals experience a wide range of hazards throughout their lives, freshwater spawning and rearing habitat is still an important factor that controls the number of sea-migrating smolt (Nehlsen *et al.* 1991, Heggenes *et al.* 1999). Small streams are important as rearing habitat for both stationary and anadromous juvenile brown trout (*Salmo trutta*; Jonsson *et al.* 2001). The abundance of juvenile salmonids in streams is a function of many factors, such as the abundance of newly emerged fry, quantity and quality of suitable habitat, abundance and composition of food resources, and biotic interactions (Bjornn & Reiser 1991). Density independent factors, such as habitat quantity and quality, cover, and stochastic events, set an upper limit of the abundance (Bjornn & Reiser 1991), and the population is thought to be held at a somewhat lower level by density dependent interactions among the juveniles (Elliott 1984, 1994). Quality and condition of these freshwater habitats may thus affect productivity and population density in brown trout (Heggenes *et al.* 1999, Jutila *et al.* 2001). Dependent on biological factors such as population density, food supply, and presence of other species, temporal factors such as season and time of day, and physical factors such as type of stream, some in-stream habitat features seem important to juvenile brown trout. These features include certain bottom substrata (Heggenes 1988a), water depths (Heggenes 1988b), water velocities (Heggenes & Traaen 1988a), and cover (Heggenes & Traaen 1988b). A fairly well-established body of theory therefore exists to understand the effects of these habitat variables in relation to individual brown trout and brown trout populations.

Aquatic ecologists are increasingly viewing streams from a landscape perspective (Allan 2004) as streams are strongly influenced by the watershed through which they flow

(Hynes 1975, Vannote *et al.* 1980, Ward 1989, Gregory *et al.* 1991). These concepts call upon a more comprehensive view of stream ecosystems by taking into account the influencing, or even controlling, factors of the surrounding watershed and riparian zone. On a conceptual level, geology, topography, and climate regime at large spatial scales influence the geomorphic processes that shape stream channels at the intermediate scale, which in turn control the in-stream habitat for aquatic biota (Frissell *et al.* 1986, Armstrong *et al.* 1998). A *watershed* (also called catchment, basin, or drainage) is a topographically and hydrologically defined unit that thus serves as the largest spatial unit under this approach. Geological conditions in the watershed particularly influence salmonid rearing habitat potential by constraining the morphological characteristics of stream reaches (Burnett 2001, Pess *et al.* 2002, Montgomery 2004). On the spatial scale of individual stream reaches, the *riparian* zone provides allochthonous energy (Murphy & Meehan 1991), cover (Bjornn & Reiser 1991), physical structure in the stream (Dahlström 2005), and retention of sediments and nutrients from upland sites (Lowrance *et al.* 1985, Myers *et al.* 1985). The condition of the riparian zone is therefore important to stream biota in terms of both structure and function of the stream habitat (Gregory et al 1991, Naiman & Décamps 1997).

In addition to natural factors, human land use practices across multiple spatial scales, such as agriculture (Roth *et al.* 1996), urban developments (Wang *et al.* 2001) and logging (Hicks *et al.* 1991), are documented to alter stream habitat and biota by disrupting the geomorphic processes that create and maintain the heterogeneous stream environment. This happens through several principal mechanisms (Allan 2004), including sedimentation and nutrient enrichment (Johnson *et al.* 1997, Jones *et al.* 2001, Meador & Goldstein 2003), contaminant pollution (Myers *et al.* 1985), hydrologic alteration (Allan *et al.* 1997, Wang *et al.* 2001), and riparian clearing and loss of large woody debris (Richards *et al.* 1996, Montgomery & Piégay 2003). Land use effects on stream conditions are also scale-dependent, by which in-stream habitat structure and organic matter inputs are typically determined by riparian conditions whereas sediment and nutrients supply, hydrology, and channel morphology are influenced primarily by watershed characteristics (Allan *et al.* 1997).

Because of their effects on growth, survival and reproduction of individuals in a cohort, local environmental conditions are clearly important in determining the production of brown trout populations (Wootton 1999). However, large-scale physical factors and land use practices control the distribution of site-specific stream habitat characteristics such as substrate, depth, water velocity, and woody debris (Richards *et al.* 1996, Wiley *et al.* 1997, Johnson *et al.* 2000). The observed response of stream organisms to habitat features can therefore be viewed as scale dependent: fine-scale observations or experiments of habitat utilization or distributions of stream organisms are influenced by factors acting on broader spatial scales (Hicks *et al.* 1991), and the fine-scale results cannot easily be extrapolated to broader scales because patterns and processes change with scale (Wiens 2002). Understanding the distribution and abundance of any species relative to habitat factors thus requires a multiscale approach (Wiens 1989), which is beginning to receive increased recognition in fisheries research as well (Wiley *et al.* 1997, Baxter & Hauer 2000, Burnett 2001, Feist *et al.* 2003, Smith & Kraft 2005). In terms of management and conservation of stream fish and restoration of their habitats, it is important to know by which factors (i.e. natural vs. land use) and at which spatial scale (watershed vs. in-stream habitat) the population is influenced, and the direction and magnitude of these factors (e.g. Johnson & Gage 1997, Fausch *et al.* 2002). To the author's knowledge, no studies have investigated the multiscale habitat relationships of juvenile brown trout.

This thesis relates density of juvenile brown trout to the physical surroundings of their summer rearing habitats at three spatial scales: the in-stream habitat, the immediate terrestrial surroundings, and the watershed. Summer low-flow conditions are critical in the sense that fish are constrained to reduced wetted areas (Magoulick & Kobza 2003), and the surrounding landscape is likely to affect the suitability of these habitats accordingly (Gregory *et al.* 1991). I expect the variation in fish density to be influenced by watershed-wide geomorphological constraints, land use, and habitat-structuring factors of the riparian area, all potentially influencing the in-stream physical habitat and the abundance of juvenile brown trout. I will therefore first model the density in relation to their surroundings at all three spatial scales, using an information-theoretic approach first developed by Akaike (1973), and extended by Burnham & Anderson (2002). Secondly, evidence in favor of each spatial scale will be compared to assess their relative influence. Thirdly, I will briefly discuss the utility of such an approach in terms of management and restoration of small streams used by salmonids. Finally, I will discuss some management implications of my findings.

Methods

Study area

The Numedalslågen River Basin drains an area of 5576 km^2 of south-central Norway, from the slopes of the Hardangervidda Plateau in the west to its estuary in the Oslofjord in the east. The main valley was eroded by glaciers and consequently has a wide cross-section through which the Numedalslågen River meanders. The Numedalslågen River is regulated for hydropower, and the lower hydroelectric powerstation at Hvittingfoss is a barrier to migrating anadromous fish. Water quality parameters during the past four years below Hvittingfoss were highly variable: totP (7-29 µg/l), totN (136-338 µg/l), turbidity (0.7-5.3 FTU), pH (6.7-6.9), and thermostable coliform bacteria (36-859 pr 100ml) (Rukke 2006). The river supports populations of some 15 fish species of the families *Salmonidae*, *Cyprinidae*, *Osmeridae*, *Gasterosteidae*, *Percidae*, *Esocidae*, and *Petromyzonidae* (Aasestad 1999). I studied 12 second- to fourth order tributary streams in the lower 71 km of the Numedalslågen River, below the Hvittingfoss hydroelectric powerstation (59°05'-59°28'N, 9°48'-10°05'E; Figure 1). The watersheds ranged in size from 1.30 to 23.1 km^2. Yearly average air temperatures ranges from 4.8°C in the upper part to 5.7°C in the lower part of the study area, with corresponding precipitation values of 1050 mm and 1025 mm, respectively (Norwegian Meteorological Institute 2006). The watersheds are situated in the boreo-nemoral and south-boreal vegetation zones with a mix of coniferous and deciduous forests (Moen 1998). Land use is dominated by cereal fields, with some rowcrop and grazing fields for cattle interspersed (range 3 - 42 % of the watershed areas). The entire area is underlain by Permian bedrock of the Monzonite-Syenite group, and various surface-geological materials.

Study design

This study investigates relationships between juvenile brown trout density in sections of streams and their surroundings at three spatial scales: 1) the in-stream physical habitat, 2) the immediate terrestrial surroundings, and 3) the parts of the watershed draining to the lowermost stream section where fish were present. The notation used here for these three spatial scales is the in-stream, reach buffer, and watershed scale, respectively. The first spatial scale refers to aquatic habitat whereas the latter two describe the terrestrial surroundings of the stream section. The 12 watersheds were chosen to reflect a gradient of physiographic

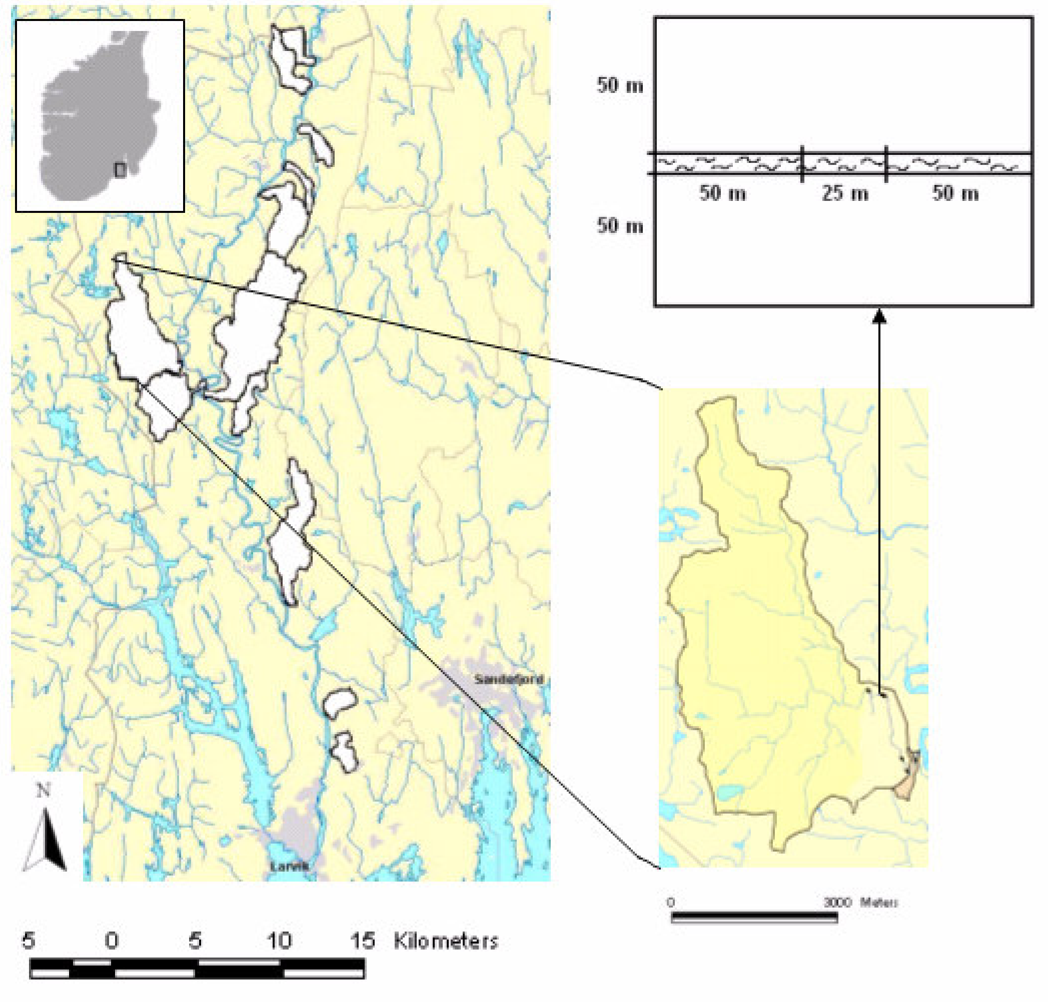


Figure 1. The location of the 12 study watersheds in the lower Numedalslågen Basin (lower left), and the location of the lower Numedalslågen Basin in southern Norway (upper left). Black segments indicate the investigated stream sections (lower right) along with the surrounding reach buffer (schematic drawing in upper right corner) in a sample watershed.

conditions and land use in the lower sections of the Numedalslågen River Basin. I sampled a median of five sections in each of the 12 streams during summer low-flow conditions in late July and August 2005. The sections were spaced over the course of suitable habitat (decision based on studying 1:50.000 topographic maps and field examination of stream width, depth, and gradient) within reach of anadromous brown trout. During the surveys on site, I recorded fish abundance, physical in-stream habitat, and terrestrial surroundings at the reach buffer scale. Watershed-scale data were extracted from existing databases using GIS.

Fish observations

Fish were observed and counted visually from the bank during daylight hours. At each designated stream section, I crawled along the stream bank and counted the number of juvenile brown trout for 20 minutes at chosen pools. I focused only on fish < 10 cm as these were deemed juveniles based on the existing literature and because they were not caught for explicit aging. Polaroid shade glasses were used when the water-surface glare was obstructing clear observations of the entire water column. Care was taken to minimize detection by the fish. After each session, I measured the wetted area of the observed pools in order to obtain a density estimate. Density was measured as the number of juveniles pr m^2 pool habitat.

Visual observation from the stream bank can be troubled by factors such as water-surface glare, turbulence, low water clarity, depth, cryptic coloration of the fish, use of cover by fish, and flight response before the fish is observed. However, visual stream bank counting is an appropriate sampling method for cutthroat fry (Bozek & Rahel 1991) and brown trout (Heggenes 1988b, Heggenes *et al.* 1990) under the conditions evident in this study. There were two main reasons for picking such a sampling approach. First, the objectives of this study were to describe the variation in juvenile brown trout density in pools, not to estimate the absolute densities over the course of entire stream sections. Second, the observations were done in pool habitats during summer low-flow conditions with good daylight conditions, clear water, and plenty of streamside vegetation to hide in. Further, the streams were narrow, shallow, and gently flowing, with no turbulence in the pools. The fish were therefore spotted easily from the banks, so that underwater counts were considered unnecessary. It is likely that electrofishing these small streams would have frightened the fish (Heggenes *et al.* 1990), because there was only moderate water velocity and clear water at the sampled stream sections. There is also a lower probability of catching small fish than large fish (Bohlin *et al.* 1989, Borgstrøm & Skaala 1993), which conflicts with the objective of this study. Also, because the streams were chosen to reflect a gradient of surface geology and land use, it is likely that variation in electrolyte content could confound density estimates. Mounting evidence of detrimental effects of electrofishing on salmonid mortality, physiology, behavior, and health calls upon restrictions of use whenever possible (Snyder 2003).

Derivation of explanatory variables

In-stream physical habitat

For the entire 25 m stream section I measured the mean bankfull width and counted the total number of pools and the number of pools formed by large woody debris (LWD, > 5cm in diameter and 1m in length). I visually estimated proportion of fine sediments (< 7mm) and coarse pebble substrate (20-65 mm) and measured the depth of the pools where trout were observed (Table 1). In-stream habitat data are provided in Appendix 1.

Table 1. Definitions of potential explanatory variables of juvenile brown trout density on multiple spatial scales.

Variable	*Definition*	*Reference study*
In-stream habitat scale		
Stream width	Mean bankfull width of the stream section (m)	Eklöv *et al.* 1999
No. LWD pools	Count of pool-forming LWD in 25 m stream section (#)	Sundbaum 2001
% LWD pools	Proportion of the total number of pools in the stream section which are formed by LWD (%)	Sundbaum 2001
Fine sediments	Proportion of fish-bearing pools covered with < 7 mm substrate (%)	Heggenes 1988a
Coarse pebble	Proportion of fish-bearing pools covered with 20-65 mm substrate (%)	Heggenes 1988a
Depth	Depth of fish-bearing pools (m)	Heggenes 1988b
Reach buffer scale		
Riparian width	Width of pristine riparian vegetation (m)	Lowrance *et al.* 1985
Variability of riparian width	Difference between the maximum and the minimum widths of pristine riparian vegetation (m)	Lowrance *et al.* 1985
Forested	Proportion of buffer with forest, all forest types (%)	Pess *et al.* 2002
Logged	Proportion of buffer which is logged (%)	Hicks *et al.* 1991
Agriculture	Proportion of buffer covered by agricultural fields (%)	Pess *et al.* 2002
Grazing	Proportion of buffer covered by grazing area (%)	Thornley & Bos 1985
Impervious surfaces	Proportion of buffer covered by roads or other impervious surfaces (%)	Wang *et al.* 2001
Watershed scale		
Watershed area and topography		
Area	Total area of the watershed (km^2)	Jutila *et al.* 2001
Gradient*	Gradient of the lower 750 m of the fish-bearing sections of the stream section (%)	Feist *et al.* 2003
Surficial geology proportions upstream of lower fish-bearing stream section (NGU-types in parentheses)		
Moraine*	Moraine material (glacial till) (11, 12, 15)	Richards *et al.* 1996
Marine deposits	Marine derived sedimentary deposits (41, 42, 43)	Feist *et al.* 2003
Fluvial deposits	Sedimentary deposits from rivers and ancient glacial rivers (20, 50)	Baxter & Hauer 2000
Weathered- and land-slide derived material	Material derived from rock disintegration and land-slides (70, 71, 72, 80)	Steel *et al.* 2004
Peat and bog	Peat and bog (90)	Jutila *et al.* 2001
Bedrock*	Bedrock, no surface geological materials (130)	Pess *et al.* 2002
Land use and land cover proportions upstream of lower fish-bearing stream section		
Populated	Rural, urban, and residential areas	Wang *et al.* 2001
Infrastructure	Roads (paved and gravel), parking lots, railroads, and other infrastructure, (semi) impervious surfaces	Thompson & Lee 2000
Water surfaces	Surface area of streams and lakes	Smith & Kraft 2005
All forest types	Total forested area	Jutila *et al.* 2001
Highly productive forest*	Highly productive forest (> 500 m^3/km^2/year; NIJOS 2005)	Jutila *et al.* 2001
Agricultural fields	Cereal and vegetable fields	Steel *et al.* 2004
Fertilized grazing fields	Fertilized areas used for livestock grazing	Thornley & Bos 1985

Variables given with an asterisk (*) were included in the set of watershed-scale models.

Reach buffer land use and land cover

I recorded land use and land cover characteristics in a 50 m wide buffer on each four sides of the stream section, constituting a rectangle of 100 m*125 m. I surveyed transects at both ends of the stream section and at both 50 m downstream and upstream from the section. Based on these distance data, I calculated the proportions of different land cover types in the 100 m*125 m reach buffer (Table 1). Characteristics of the riparian land cover included in the analyses all had the potential to influence the in-stream environment, and in turn affect juvenile brown trout density and distribution (Gregory *et al.* 1991, Allan *et al.* 1997, Naiman & Décamps 1997). Reach buffer data are provided in Appendix 2.

Watershed topography, geology, land use, and land cover

Landscape properties that contribute most directly to the structure and function of stream ecosystems include catchment land use and land cover, channel slope, and quaternary and bedrock geology (Allan *et al.* 1997, Wiley *et al.* 1997, Johnson & Gage 1997). For juvenile salmonids, quality of the in-stream physical habitat is largely determined by depth, velocity, substrate, and cover (e.g. Heggenes 1988b, Bjornn & Reiser 1991). The landscape characteristics included in the analyses all had the potential to influence the in-stream environment, and in turn affect juvenile brown trout density and distribution. Watershed characteristics are given in Appendix 3.

Stream gradient: All sampled stream sections were site-referenced on the program MapSource 4.09 (Garmin Inc. 2002). Using the program, I created a new plot 750 stream-meters above the lowermost fish-bearing stream section. At both plots I estimated elevation by effectively assuming a homogenous gradient in that contour interval and assigned elevation accordingly based on the distance to the lower contour. The gradient from 750 m above the lower fish-bearing reach was then calculated as the difference in elevations over the 750 m course of the stream, and measured as percent slope (Table 1).

Watershed delineation and area calculation: For each watershed, I manually delineated the outer (the entire watershed) and the inner boundaries (referring to the area draining to the lowermost fish-bearing stream section) of the watershed on 1:50,000 topographic maps (Norwegian Mapping Authority) using ArcView 3.2 (ESRI 2001) (as in Wang *et al.* 2001). I followed the watershed divides of the official register for watersheds (REGINE) wherever possible. The resulting polygons, consisting of an outer and an inner boundary, were used in subsequent overlay analyses of watershed surficial geology, land use, and land cover. I used the map tool Kartulf provided by the Norwegian Water Resources and Energy Directorate (NVE) in order to calculate the area of the entire watershed (Table 1) and the parts of the watershed draining to the lower fish-bearing stream section. I calculated the area of the watershed draining to the lower fish-bearing stream section to control the calculation of the area of surficial geology, land use, and land cover types.

Surficial geology: I used quaternary geological maps provided by the Geological Survey of Norway (NGU) as the basis for an overlay analysis with watershed boundary maps in ArcView 3.3 (ESRI 2002). I recorded the area covered by each specific surface geological type (denoted "NGU type" in Table 1) within the parts of the watershed draining to the lowermost fish-bearing stream section. I pooled the different types of surface geological materials into 6 categories based on material origin and likely influence on in-stream habitat by means of infiltration and groundwater potential. The measure is thus given as the percentage of the watershed draining to the lowermost fish-bearing reach that contains the given surface geological category (Table 1).

Land use and land cover: The County Governor of Vestfold provided land use and land cover data for the watersheds by doing an identical overlay analysis as described above based on digital land use/cover maps managed by the Norwegian Institute of Land Inventory (NIJOS). The analysis was conducted in ArcView 3.2. The land use and land cover variables derived from this analysis are described in Table 1. A few variables were omitted from the analysis due to their limited spatial distribution or redundancy with surface geological features. All variables are given as proportion of the parts of the watershed draining to the lowermost fish-bearing reach.

Modeling approach and development of candidate models

Modeling approach

I followed a two-stage modeling approach. First, I developed a set of watershed-scale regression models to explain the variation in mean density across all fish-bearing streams. Regression modeling is a common analytical approach in landscape-scale studies (Johnson & Gage 1997). I then made predictions for each stream based on their watershed characteristics, using the weighted evidence of these watershed models (Burnham & Anderson 2002). The second stage was to model the residual variation in fish density at the stream sections using in-stream and reach buffer variables. The residual variation in juvenile brown trout density was defined as the difference between the observed density at any particular stream section and the multimodel-estimated density of that stream. This was done to tackle the inherent pseudoreplication issues (Hurlbert 1984) of landscape-level studies (Johnson & Gage 1997), and because different processes act on different spatial scales (Wiens 2002). This study concerned only densities, and not presence/absence. Consequently, I only included stream sections where juvenile brown trout were present in the analyses.

Regression models across multiple spatial scales

The first step of the two-stage modeling approach involved modeling the mean density of juvenile brown trout across all fish-bearing streams. Due to the low number of streams, it was necessary to pre-screen the predictor variables to keep the number of models low to avoid "spurious effects" (Anderson *et al.* 2001a). I expected geological factors that control stream morphology to be the most influential. In addition, I ranked the information contribution by all the individual explanatory variables by examining the scatterplot and the simple coefficient of determination (r^2) of each variable regressed against mean trout density. I retained the following explanatory watershed-scale variables: moraine, bedrock, gradient, and highly productive forest. These variables were combined into *a priori* multiple regression models of mean juvenile brown trout density (Table 3).

At the reach buffer and in-stream scales I modeled the residual density, i.e. the difference between observed density at any given reach and the watershed-models-predicted density for the whole stream. I developed two sets of *a priori* multiple regression models to explain the residual variation in fish density by using reach buffer (Table 5) and in-stream habitat (Table 7) variables, respectively, in sections where juvenile brown trout were present. I used Minitab 14.20 statistical software (Minitab Inc. 2005) in all the data analyses.

Model analyses: the information-theoretic approach

Model selection criterion

Because trivial null hypothesis testing is uninformative (Anderson *et al.* 2000), subjective (Berger & Berry 1988), and logically wrong in observational studies (Cohen 1994, Ellison 1996), this study adopted the information-theoretic approach first developed by Akaike (1973) and applied to ecological research by Burnham & Anderson (2002) in order to find the relative plausibility of the *a priori* candidate models at each spatial scale. Information-theoretic data analysis is based on Kullback-Leibler information, which is the information lost when statistical (i.e. fitted) models are used to approximate full truth (Kullback & Leibler 1951). Akaike (1973) found a formal relationship between Kullback-Leibler (K-L) information and maximum likelihood (ML) theory, which makes it possible to optimize parameter estimation and model selection for a given dataset (Anderson *et al.* 2000). Akaike's information criterion (*AIC*) is given as:

$$AIC = -2\log_e(\ell(\hat{\theta} \mathrm{I} data)) + 2K ,$$

where $\log_e(\ell(\hat{\theta} \mathrm{I} data))$ is the value of the maximized log-likelihood over the unknown parameters (θ) given the data and the model, and K is the number of estimable parameters in that approximating model. I used least squares (LS) estimations, for which *AIC* is expressed as:

$$AIC = n\log(\hat{\sigma}) + 2K ,$$

where

$$\hat{\sigma} = \frac{\sum \hat{\varepsilon}_i^{\,2}}{n} \text{ (the ML estimate of } \sigma^2\text{)},$$

and $\hat{\varepsilon}_i$ are the estimated residuals for a particular candidate model. K is the number of estimable parameters, including the intercept and error variance, and n is the sample size. I used the small-sample adjusted criterion (*AICc*) (Hurvich & Tsai 1989, Burnham & Anderson 2002) in all three model selection efforts. *AICc* is given as:

$$AICc = AIC + \frac{2K(K+1)}{n-K-1}$$

AICc exhibits the same qualities as the ordinary criterion and the notations are therefore used interchangeably. The model for which *AIC* is minimal is selected as best for the given data. The models i were ranked using the simple *AIC* differences, Δ_i, given as $\Delta_i = AIC_i - AIC_{min}$, where the AIC_{min} denotes the best approximating model (i.e. the model with the lowest *AIC* value). The larger the Δ_i value, the less plausible is the fitted model i as the best approximating model in the candidate set (Burnham & Anderson 2001). To make interpretation and inference easier, the likelihood functions of the models were normalized so that they sum to 1. The probability of model *i* being the K-L best model in the set is called the Akaike weight *w*, and is given as:

$$w_i = \frac{\exp(-\frac{1}{2}\Delta_i)}{\sum_{r=1}^{R}\exp(-\frac{1}{2}\Delta_i)}$$

I estimated the average density ($\overset{\Delta}{D}$) of juvenile brown trout for each of the fish-bearing streams using a model-averaged multimodel inference approach for the set of watershed-scale models (Burnham & Anderson 2002). Predictions can be made from more than one model by simply weighting the predictions from each model with its Akaike weight (w_i):

$$\overset{\Delta}{D} = \sum_{i=1}^{R} \hat{w}_i \hat{D}_i$$

The density estimate ($\overset{\Delta}{D}_i$) for a given stream was thus weighted among the models $i=1,2,..,R$ in the set of candidate models.

Model selection output

The model selection results were reported as recommended by Anderson *et al.* (2001b), with tables showing the number of estimable parameters (K), the residual sum of squares (RSS), the maximized log-likelihood function ($log(\ell)$), the model selection criterion ($AICc$), the simple differences (Δ_i), and the Akaike weights (w_i) for the models in the candidate set. Interpretation and inference is based chiefly on the Akaike weights. I only provided parameter estimates for those models in each set which obtained some substantial relative support. I used an evidence ratio of five as a cut-off (i.e. $w_{max}/w_i < 5$). For these models I presented the estimated standard error of the model (s, the square root of the estimated variance), the Akaike weight (w_i), the least-squares parameter estimates (β-coefficients) and their associated standard errors (SE), and the multiple coefficient of determination (R^2).

Results

Juvenile brown trout distribution

Juvenile brown trout were found in pool habitats in 11 (92%) of the 12 tributary streams in this study, and at 33 (61%) of the 54 sections investigated. The observation from one stream section was excluded from further analyses. At that section (in the stream Gavelstad) there was an exceptionally high density (4.13 trout m^{-2}), probably due to groundwater upwelling (NGU type 50; fluvial deposits). However, inclusion of that observation resulted in poor model fit and difficult interpretation of the models. Analyses of juvenile brown trout density in relation to the surrounding habitat and landscape were therefore restricted to encompassing a total of 32 sections in 11 streams (Table 2).

Table 2. Summary table of juvenile brown trout densities observed in pool habitats in each of the fish-bearing tributary streams (n=11) of the lower Numedalslågen River during summer low-flow conditions 2005, and model-averaged predictions for mean density. The streams are organized so that the latter stream is closest to the estuary.*

Stream name	*No. sections investigated*	*No. sections present*	*Mean density in stream (range) no./m^2*	*Predicted density no./m^2*
Otterstad	4	2	0.47 (0.27-0.67)	0.74
Styrmobekken	5	5	0.61 (0.25-1.00)	0.43
Pinnestad	5	4	0.76 (0.40-1.25)	0.90
Lindsverk	3	3	1.31 (1.00-1.67)	1.03
Gavelstad	6	3	0.89 (0.50-1.67)	0.87
Røsholt	5	4	0.37 (0.08-0.75)	0.45
Kringlemyr	5	4	0.27 (0.04-0.63)	0.35
Haugselva	5	2	0.53 (0.05-1.00)	0.55
Hvarnesdalen	3	1	0.75 (0)	0.48
Almedalen	5	2	0.33 (0.05-0.60)	0.33
Hedrum	5	2	0.16 (0.14-0.17)	0.29

* One outlier was not included in this table and omitted from further analyses.

Modeling results

Variation between streams – the watershed scale

Watershed-scale models were used to explain the variation in average juvenile brown trout density across the 11 fish-bearing streams (Table 3). Only variables referring to “natural” land cover (highly productive forest), topography (gradient), and geology (bedrock and moraine) were retained from the variable screening. Variables referring to anthropogenic land use were poor predictors of average fish density compared to the natural variables, and were consequently not included in the modeling.

Table 3. Model selection results from the watershed-scale analysis of mean juvenile brown trout density. The models were based on observations in pool habitats in each of the fish-bearing tributary streams (n=11) of the lower Numedalslågen River during summer low-flow conditions 2005.

Model	*K*	*RSS*	*Log(ℓ)*	*AICc*	Δ_i	w_i
Moraine	3	0.4029	-18.1883	-26.9480	0	0.5547
Moraine + gradient	4	0.2998	-19.8139	-24.9612	1.9868	0.2054
Moraine + HP forest	4	0.4015	-18.2074	-21.7482	5.1998	0.0412
Moraine + HP forest + interaction	5	0.1989	-22.0707	-22.1413	4.8067	0.0502
Bedrock + bedrock^2	4	0.3215	-19.4296	-24.1925	2.7555	0.1399
Moraine + gradient + HP forest	5	0.2739	-20.3109	-18.6218	8.3263	0.0086
Global	8	0.07499	-27.4356	33.1287	60.0768	0.0000

Abbreviation: HP forest = highly productive forest. Explanations of the variables are found in Table 1.

The three best approximating models received considerable absolute support (i.e. multiple coefficient of determination, R^2; Table 4). The linear relationship between percent moraine in the watershed and average density was the best approximating model in the candidate set (Figure 2). For every percent increase in watershed moraine cover (range 0 – 59.7%), the average density in the stream was estimated to increase by approximately 0.012 fish pr m^2.

Table 4. Characteristics of the three best approximating watershed scale models.Abbreviations for the explanatory variables are as follows: moraine (mor), gradient (grd), and bedrock (bed).

Model structure	*SE*	w_i	β_0 *(SE)*	β_1 *(SE)*	β_2 *(SE)*	R^2
$\beta_0 + \beta_1(\text{mor})$	0.2116	0.5547	0.2653 (0.1037)	0.01172 (0.003007)		0.628
$\beta_0 + \beta_1(\text{mor}) + \beta_2(\text{grd})$	0.1936	0.2054	0.2192 (0.09887)	0.008689 (0.003301)	0.05726 (0.03451)	0.723
$\beta_0 + \beta_1(\text{bed}) + \beta_2(\text{bed}^2)$	0.2005	0.1399	1.6160 (0.2537)	-0.04601 (0.01296)	0.0004248 (0.0001468)	0.703

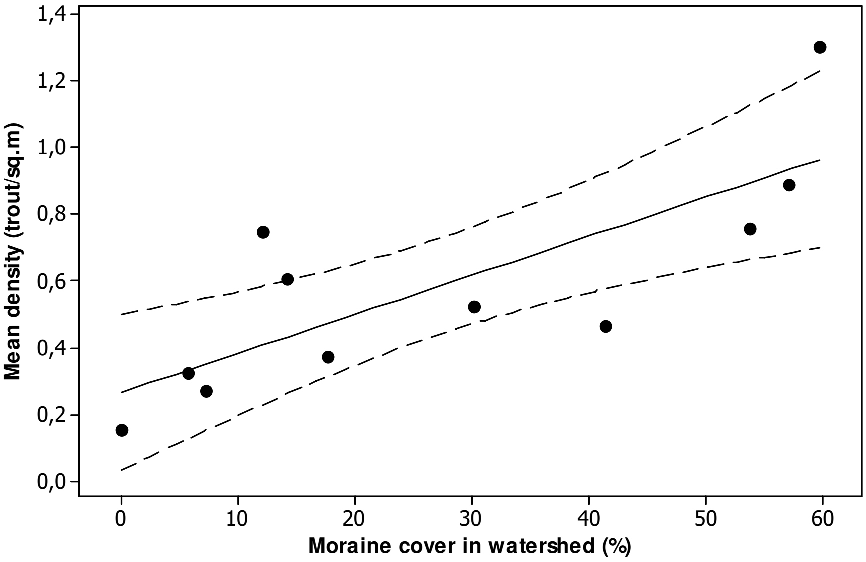


Figure 2. Relationship between proportion of the watershed covered by moraine materials and the mean density of juvenile brown trout in pool habitats in 11 tributary streams of the lower Numedalslågen River during summer low-flow conditions, 2005. Dotted lines denote 95 % C.I.

Residual variation in streams – the reach buffer scale

Model selection results for the *a priori* models for reach buffers are shown in Table 5. Models containing land use variables (agricultural fields and logged areas) performed better than those of natural vegetative cover (proportion forested and width of riparian vegetation).

Table 5. Model selection results from the reach buffer analysis, relating residual juvenile brown trout density in pool habitats in 32 stream sections during summer low-flow conditions to reach buffer land use and land cover in the lower Numedalslågen Basin, 2005.

Model	*K*	*RSS*	*Log(ℓ)*	*AICc*	Δ_i	w_i
Riparian width + riparian width^2	4	3.8151	-34.0283	-58.5751	3.4862	0.0659
Forested + forested^2	4	3.7877	-34.1436	-58.8058	3.2556	0.0739
Logged + logged^2	4	3.6476	-34.7467	-60.0118	2.0495	0.1351
Agriculture + grazing + impervious	5	3.5327	-35.2588	-58.2099	3.8515	0.0549
Riparian variability + agriculture + interaction	5	3.1921	-36.8809	-61.4541	0.6072	0.2778
Riparian width + riparian variability + interaction	5	3.8183	-34.0149	-55.7221	6.3393	0.0158
Riparian variability + logged + interaction	5	3.1321	-37.1845	-62.0613	0	0.3764
Global	11	2.4323	-41.2304	-47.2608	14.8006	0.0002

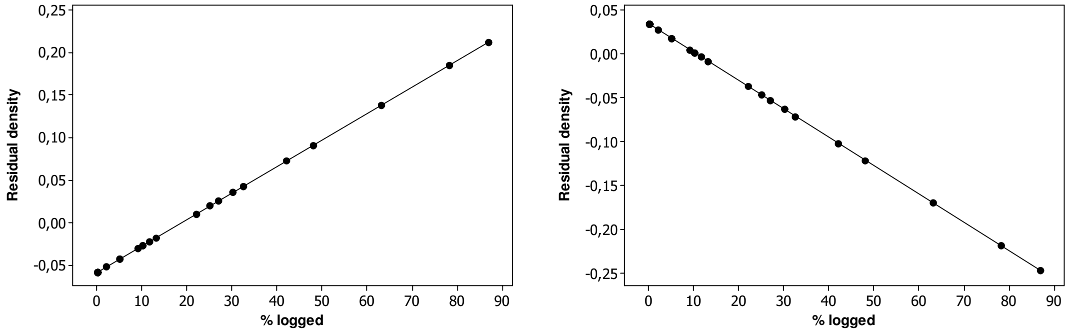
Explanations of the variables are found in Table 1.

Interaction models with variability if riparian width in relation to either agriculture or logged areas had a greater relative support than the other models (Table 6). A quadratic function of the proportion of the buffer being recently logged was a weak, third best model. The models explained only modest amounts of absolute variation of residual brown trout density.

Table 6. Characteristics of the three best approximating reach buffer models. Abbreviations for the explanatory variables are as follows: variability of riparian width (var), logged (log), and agricultural fields (agr).

Model structure	*SE*	w_i	β_0 *(SE)*	β_1 *(SE)*	β_2 *(SE)*	β_3 *(SE)*	R^2
$\beta_0 + \beta_1(\text{var}) + \beta_2(\text{log}) + \beta_3(\text{var*log})$	0.3345	0.3764	-0.05790 (0.1097)	0.005553 (0.004259)	0.003104 (0.003050)	-0.0003839 (0.0001567)	0.182
$\beta_0 + \beta_1(\text{var}) + \beta_2(\text{agr}) + \beta_3(\text{var*agr})$	0.3376	0.2778	0.1639 (0.1372)	-0.009520 (0.005038)	-0.005920 (0.003459)	0.0004444 (0.0001902)	0.166
$\beta_0 + \beta_1(\text{log}) + \beta_2(\text{log}^2)$	0.3547	0.1351	0.05553 (0.08456)	-0.009720 (0.008110)	0.0001230 (0.0001076)		0.047

The riparian variability-logging interaction model was 1.35 times more plausible than the second best approximating model. The change in residual density of a 1-unit change in variability of riparian width also depended on the size of the proportion of the reach buffer which was logged (Figure 3). When there was no variability of riparian width the residual density increased by 0.003 fish pr m^2 for every percent increase in the proportion logged. Holding the riparian variability constant at the median of 16.5 m, the residual fish density in the corresponding stream section decreased by 0.03 juvenile brown trout pr m^2 for every percent increase in logged reach buffer area.



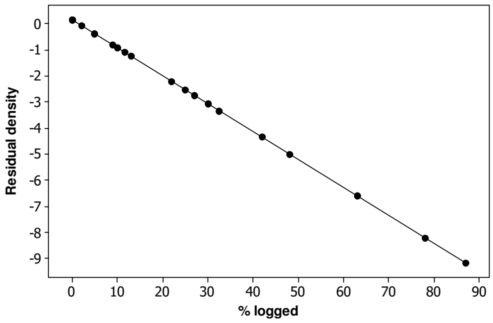


Figure 3. Residual density of juvenile brown trout in pool habitats during summer low-flow conditions in relation to percentage logged of the reach buffer when holding the variability of riparian width constant at 0 m (upper left), 16.5 m (the median; upper right), and 39.5 m (third quartile; lower plot) in 32 stream sections of 11 fish-bearing tributaries of the lower Numedalslågen River. The plots are predicted residual densities from the best approximating reach buffer model and confidence intervals are consequently not included. Note differences in y-axes.

Residual variation in streams – the in-stream habitat scale

Among the in-stream habitat models, the depth-model proved to be the best approximating model (Table 7). Models referring to the amount of lateral habitat (stream width) and the formation of pool habitat (LWD-models) performed poorly in a relative and absolute sense. Composite models of both the formation and the actual in-stream environment did not receive sufficient support to be deemed good approximating models.

Table 7. Model selection results from the in-stream habitat analysis, relating residual juvenile brown trout density in pool habitats in 32 stream sections to in-stream habitat features during summer low-flow conditions in 11 tributary streams of the lower Numedalslågen River, 2005.

Model	*K*	*RSS*	*Log(ℓ)*	*AICc*	Δ_i	w_i
Width + fine sediments	4	3.7206	-34.4296	-59.3777	11.1154	0.0038
Depth + coarse pebble + interaction	5	3.4262	-35.7485	-59.1894	11.3038	0.0034
No. LWD pools + depth	4	3.5237	-35.2996	-61.1177	9.3755	0.0090
No. LWD pools + coarse pebble	4	3.6169	-34.8819	-60.2823	10.2109	0.0059
Depth + depth^2	4	2.6288	-39.9873	-70.4932	0	0.9739
Width + depth + interaction	5	3.5548	-35.1590	-58.0103	12.4829	0.0019
% LWD pools + width + depth + coarse pebble	6	3.4054	-35.8460	-56.3320	14.1612	0.0008
Global	11	1.7792	-46.2332	-57.2663	13.2269	0.0013

Explanations of the variables are found in Table 1.

The best approximating model at the in-stream habitat scale was a quadratic function of depth (Table 8). This single model received substantial support among the candidate models ($w_i >$ 0.90), and was therefore the only one explained in further detail. The coefficient of the second order term of depth was negative, which means a downward concavity (Figure 4). In depths between 25 cm and 44 cm there were higher densities of juvenile brown trout than predicted for the stream overall.

Table 8. Characteristics of the best approximating in-stream habitat scale model. Abbreviation for the explanatory variable is depth (dep).

Model structure	*SE*	w_i	β_0 *(SE)*	β_1 *(SE)*	β_2 *(SE)*	R^2
$\beta_0 + \beta_1(\text{dep}) + \beta_2(\text{dep}^2)$	0.3011	0.9739	-2.1068 (0.7711)	13.6210 (4.5060)	-20.1190 (6.2040)	0.313

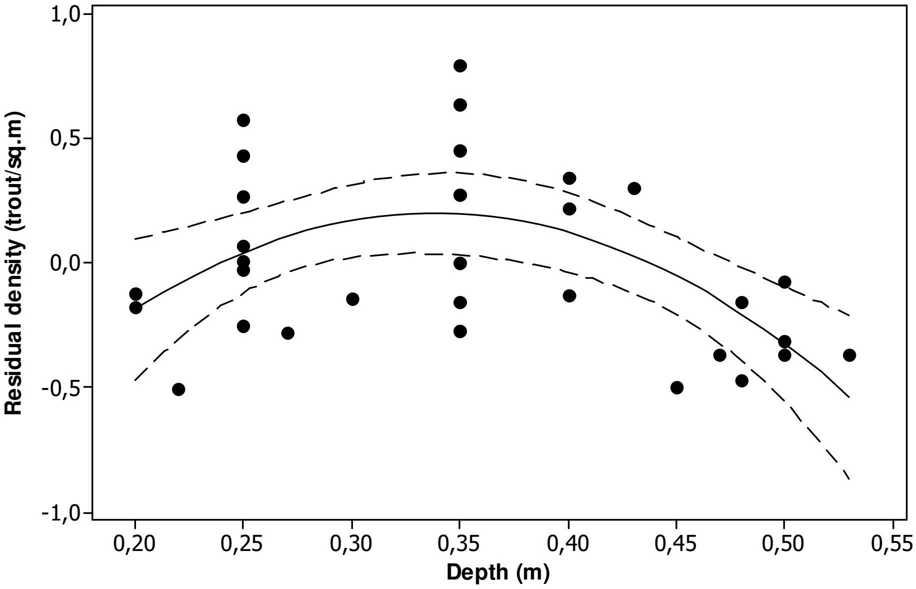


Figure 4. Residual juvenile brown trout density in relation to pool depth in 32 stream sections in 11 tributary streams of the lower Numedalslågen River during summer low-flow conditions, 2005. Dotted lines denote 95 % C.I.

Comparison of performances of the best approximating models

Comparing the *total amount of variation* in juvenile brown trout density explained by the best approximating model for each of the three spatial scales showed that the watershed-best model explained more variation than did the reach buffer and the in-stream-best models (Figure 5).

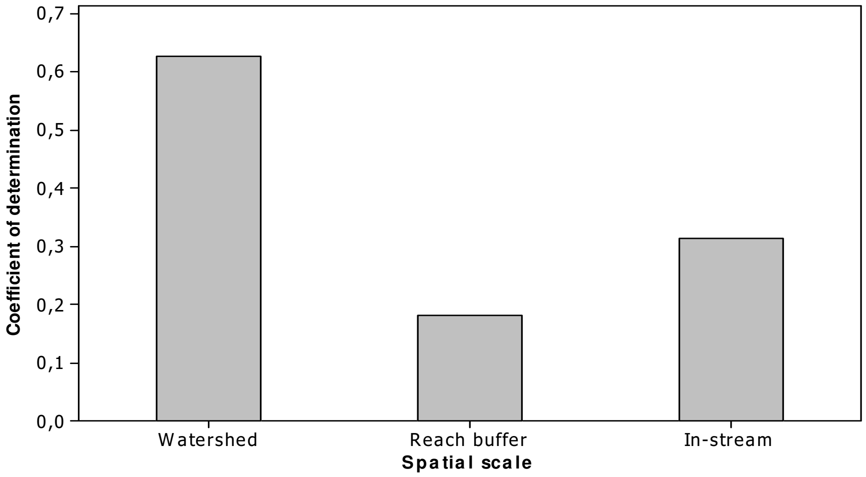


Figure 5. The amount of variation (R^2) in juvenile brown trout density explained by the single best approximating model at each of the three spatial scales.

The *plausibility* of the watershed models cannot be directly compared to the reach buffer and in-stream models because they were based on different datasets. The reach buffer and in-stream models can be directly compared by looking at their *AICc* values. By calculating the Akaike weights for the best reach buffer and in-stream models, it was evident that the latter was a better model of residual juvenile brown trout density (Table 9).

Table 9. Relative plausibility of the best approximating reach buffer and in-stream models.

Spatial scale	*Model*	*w*
Reach buffer	Variability of riparian width + logged + interaction	0.01
In-stream	Depth + depth^2	0.99

Explanations of the variables are found in Table 1.

Discussion

Fish observations and density – covariate relations

At least a large fraction of the juveniles were effectively assumed to be offspring of anadromous brown trout as they were found within reach of anadromous adults. It is therefore possible that the counts included both resident and anadromous juvenile brown trout. However, as both groups need the same resources for rearing (Klemetsen *et al.* 2003) it is reasonable to discuss the relationships with their multiscale surroundings as one group because the habitat factors act similarly on all the individuals and likely set an upper carrying capacity for the stream and stream section (Bjornn & Reiser 1991). The origin of the individuals was therefore not the interesting part, the total density variation in relation to the surroundings was.

The multiscaled nature of juvenile brown trout density

Watershed scale

At the watershed level, pre-screening of potential predictors retained only "natural" variables (moraine, gradient, bedrock, and highly productive forest), of which only the former three were included in the three best approximating models. The abundance of juvenile trout in streams is a function of many factors, such as the abundance of newly emerged fry, quantity and quality of suitable habitat, abundance and composition of food resources, and biotic interactions (Bjornn & Reiser 1991). Because brown trout was the only, or at least the dominant, fish species in these tributary streams, streams supporting high densities of juvenile trout likely exhibited a suite of beneficial conditions (Murphy & Meehan 1991, Bjornn & Reiser 1991). The findings should therefore be interpreted in terms of habitat quantity and quality because the study encompassed several streams over a physiographic and land use gradient within a confined region.

Geological conditions in the watershed particularly influence salmonid rearing habitat potential by constraining the morphological characteristics of stream reaches (Frissell *et al.* 1986, Pess *et al.* 2002), as well as dictating the hydrology and land use patterns in the watershed (Allan 2004). By its control over substrate size and velocity, geology has also been proven a good predictor of abundances of steelhead parr (*Oncorhynchus mykiss*; Thompson & Lee 2000) and juvenile chinook salmon (*O. tshawytscha*; Burnett 2001). Geomorphology of stream channels is an important means of understanding salmonid habitat relationships because prevailing disturbance regime is thought to shape communities by its control over habitats (Montgomery 2004). Increasing proportion of bedrock (i.e. poor or no cover of quaternary geology or top soils) in a watershed likely constrains the geomorphic freedom of stream channels, and in turn constrains the habitat heterogeneity (Gregory *et al.* 1991). In contrast, the typical finding of higher densities of salmonids in unconstrained valley segments (typically characterized by wider valleys and modest gradients) may be explained by factors such as a larger hyporheic zone, higher food production, more complex channel patterns, and accumulations of gravel and wood (Bowlby & Roff 1986, Gregory *et al.* 1991, Baxter & Hauer 2000, Burnett 2001).

Gradient is an important driver for water velocity in small streams, and exerts considerable control over channel characteristics because it adjusts more slowly than other hydraulic variables. Particularly, the velocity controls the substrate size and translocation of drifting food resources, and in that respect influences which organisms that can live on that site (Allan 1995). The positive relationships between mean density, gradient, and moraine may be because the gradients were only modest (0.3-6.5 %) in the streams investigated. However, as also noted by Thompson & Lee (2002), it was not possible to relate these structuring, underlying factors *directly* to fish density, other than saying that increasing moraine cover and gradient exhibited positive influence, and increasing bedrock cover exhibited negative influence over the resources needed for rearing juvenile brown trout.

Although natural factors were found to be the most important explanatory variables on the watershed scale, it is important to address both anthropogenic and natural features, as they are often highly collinear and their relative importance difficult to untangle (Richards 1996, Allan 2004). Human factors are the focus of management actions, whereas the natural factors provide the context for management. Allan (2004) noted that natural factors may be of primary importance when human influence in the watershed is minor, which was evidently the case in this study. This does not imply that watershed-wide human land use is unimportant. Due to the limited number of streams it was necessary to lower the number of variables, and the variables that best explained the variation in density were all “natural”.

Reach buffer scale

At the two smaller spatial scales, I modeled the residual density of juvenile brown trout. Residual density depicted the influence of local conditions in relation to the density that was expected for the entire stream (i.e. which reaches supported more or less fish than expected).

Relationships between juvenile brown trout and their surroundings also relied on correlation at the reach buffer and in-stream scales. Although the mechanisms are better known at these spatial scales (Jones *et al.* 2001), care must be taken when assuming causation.

For the best reach buffer model I found that only when the proportion of logged area was increased above 15 % and the variability of riparian width was larger than 5 m, the model predicted lower residual density. At smaller extents of both variables there was a weak positive relationship with residual density. Stream-side logging has been shown in numerous studies to decrease stream habitat quality and lower the abundance of juvenile salmonids by increasing sedimentation and nutrient runoff, increase loads of organic matter, and trigger mass wasting events (Hicks *et al.* 1991, Carignan & Steedman 2000). However, some logging and riparian clearing may enhance the carrying capacity of stream habitats on the short term, especially in northern forest streams (primarily by increasing autochthonous production by elevating solar radiation and nutrient inputs; Hicks *et al.* 1991, Jutila *et al.* 1999).

Agricultural land use in close proximity to streams is typically associated with increased sediment (Jones *et al.* 2001) and nutrient loadings (Johnson *et al.* 1997) which may deter trout habitat in the long run (Eklöv *et al.* 1999). Also, agriculture in the riparian implies a narrower belt of streamside vegetation. Riparian vegetation is known to moderate stream temperatures in summer (Gregory *et al.* 1991), provide energy inputs from the canopy (Wipfli 1997), and provide structure and cover in the form of woody debris in the streams (Dahlström 2005). In this study it seemed that the variability of riparian width was more important than the average riparian width of both sides. This makes sense in that a thick buffer of riparian vegetation on one side of the stream cannot trap nutrients and sediments, provide shade and litterfall, or stabilize the banks on the other side (Lowrance *et al.* 1985). Increased proportion of the stream-side land being logged or converted to agricultural fields while even more land is retained as buffer on the other side (reflected through increased riparian width variability) thus was associated with lower densities of trout. At this spatial scale, disturbances to the natural vegetation cover were more influential than the natural cover itself in explaining residual variation. However, due to the relatively low amount of absolute variation explained by these models one needs to be careful with using the model for predictive purposes. Of the variables and models included here, I conclude that the variation in residual density was not strongly affected by stream-side land cover or land use except at high levels of disturbance.

In-stream habitat scale

A quadratic function of depth was the only model that received any relative support among the *a priori* in-stream models. Stream reaches with 25-44 cm deep pools were likely to support greater densities of juvenile brown trout than were predicted for the whole stream. Several studies have investigated the use of in-stream habitat by juvenile brown trout, including depth. There is however a large span of results from studies relating brown trout density to depth. This is not striking given the wide array of stream environments (physical habitat, discharge, and biotic communities), sampling methods (certain stream habitats or entire stream segments), and value ranges of depth. I only made observations in pool habitats, which differs from studies investigating entire stream sections to find out where certain age groups prefer rearing (e.g. Heggenes 1988c). Brown trout prefer rearing in pools, but juvenile fish may be excluded by larger (predatory) fish and hence are restricted to more riffle-like habitat (Greenberg 1994). My findings of pool depth in relation to juvenile brown trout density correspond with results from previous research of small forest streams with larger fish being absent (e.g. Mäki-Petäys *et al.* 1997). In such streams or stream sections, the older juveniles distribute themselves according to the suitability of the habitat (Heggenes 1988d). I found young-of-the-year primarily in riffle habitats and along stream margins, most likely because they may have been excluded by older juveniles (Greenberg 1994).

Assigning depth preferences is an arguable issue also due to the high degree of collinearity with other in-stream habitat features, such as velocity, substrate, and cover. Juvenile brown trout distribute themselves in accordance with temperature and biotic factors as well (Heggenes 1988a, Heggenes & Traaen 1988b, Mäki-Petäys *et al.* 1997). Which habitat variable is the most important for juvenile brown trout density has been the focus of many studies, but might not be an important question due to the uniqueness of each site and the multivariate nature of stream habitats (Heggenes 1988b). Construction of universal habitat suitability curves for brown trout as a species based on a finite sample (e.g. Mäki-Petäys *et al.* 1997) is not possible either, as it would reveal only a glimpse of the fundamental niche of the species (Elliott 1994).

Of the factors that are deemed “the most important” habitat components in the literature, I only quantified substrate and depth. It could be argued that the other factors, such as current velocity and cover, were also important descriptors of pool habitat quality in this study system, and consequently that they should be quantified. However, current velocity varies a lot over just a few centimeters of pool habitat (Montgomery & Piégay 2003), and makes any generalization for the whole pool doubtful. By such, gradient measured at the watershed scale may be a better explanatory variable. In addition, increasing number of LWD pieces and LWD pools indicate slower currents and more pool habitat (Dahlström 2005). The number of LWD pieces also acts as a surrogate for habitat complexity and cover, and has been directly linked to abundance of juvenile brown trout (Sundbaum 2001) and other salmonids (e.g. Tschaplinski & Hartman 1983, Mossop & Bradford 2004). Further quantification of current velocity and cover was therefore not found necessary.

All spatial scales compared

Which attributes of the surroundings had the greatest influence on juvenile brown trout density was clearly a function of the scale of my observations. In general, this is a common finding in multiscale studies. Within the allowed boundaries for inference from this study, greater densities were associated with intermediate pool depths in reaches with riparian vegetation on both sides and small proportions of riparian clearcuts and agricultural fields in moraine-dominated watersheds of modest gradient. In terms of total amount of variation explained the best approximating watershed-scale models performed better than did the best in-stream and reach buffer scale models. Large-scale factors overriding more local ones is a common finding in multiscale studies of biotic integrity and biological assemblages (Roth *et al.* 1996, Rabeni 2000, Townsend *et al.* 2003), habitat quality (Richards *et al.* 1996), and water chemistry (Johnson *et al.* 1997). This is hardly any surprise because large-scale factors set the stage for smaller-scale factors to act in turn (Frissell *et al.* 1986). However, our knowledge is still incomplete because the multiscaled nature of streams and their biota has only been quantified by a limited number of studies until now. It is also important to note that the physical processes operating on stream habitats act *across* multiple spatial scales, and not just at some fixed spatial scale (Gregory 2004, Smith & Kraft 2005). The question is therefore really about the relative importance of the effects acting at the different spatial scales (Lammert & Allan 1999, Weigel *et al.* 2003).

A striking pattern was that natural models were the best at the watershed scale, whereas land-use models were the most influential at the reach buffer scale. The variation in land use and land cover was larger at the reach buffer scale, as in the study of Lammert & Allan (1999), who found reach buffer land use most influential on stream biotic integrity. On the other hand, Roth *et al.* (1996) found watershed-wide land use more important than local land use in the same river basin in Michigan, United States. This divergence may be because the former study only encompassed only three watersheds with six replicate reaches within each stream, whereas that of Roth *et al.* (1996) spanned only minimal replication within each of the 13 watersheds. My study was a compromise in that respect, with several replicates in several streams. In addition to study design, the spatial scale at which an “effect” is detected also depends on how well local land use mirrors that of the whole watershed, by data resolution, and by the relationships between human land use and the natural gradients in the region (Lowrance 1985, Allan 2004). Agricultural land uses were primarily found in close proximity to the tributary streams of the Numedalslågen River, whereas their overall watersheds were only subject to some logging. Because of the limited land use extent and chiefly natural systems, it is likely that land use was of some importance only at the reach buffer scale, and that most overall variation was explained by watershed-wide natural factors. Pool depth also described the density variation better than did riparian condition, except at high levels of disturbance.

My findings provide a quantitative means for understanding the variation in juvenile brown trout abundance among streams and within streams based on physical habitat. In turn, this suggests that there exist multiple controlling factors over juvenile brown trout abundance across multiple spatial scales in these tributary streams (Frissell *et al.* 1986, Wiens 1989, Armstrong *et al.* 1998). The inherent multivariate nature of such studies makes the underlying mechanisms unclear (Johnson & Gage 1997). However, at a heuristic level, finding good approximating models from the physical surroundings rather than universal laws, the analysis proved important insights into the multiscaled habitat relationships of juvenile brown trout in their summer rearing ranges.

Liabilities and limitations of the watershed approach

Several authors have highlighted the spatial gap between scientific contributions and the scale that fisheries managers are most often challenged (Lewis *et al.* 1996, Wiley *et al.* 1997, Fausch *et al.* 2002). Identifying the spatial scales on which physical factors act to shape stream habitat and the biota therein is an important first step before any management practice is to be initiated (Armstrong *et al.* 1998). This is especially emphasized in the literature of stream restoration ecology, where proper siting of measures to restore ecosystem function, and not only structure, depends on the surrounding watershed (Kentula 1997, Kershner 1997). There is no reason to initiate management or restoration actions on the stream section level in streams where the fish are limited by watershed-scale factors. In either case, a multiscale approach which incorporates key features of the watershed such as geology, topography, and land use in a proper analytical framework needs to be established to better understand the stream ecosystems (Johnson & Gage 1997). This study aimed at understanding the abundance and distribution of juvenile brown trout in their summer rearing habitats at multiple spatial scales, thus representing a departure from "typical" investigations in fisheries biology (Lewis *et al.* 1996, Armstrong *et al.* 1998).

Some general limitations apply to most empirical watershed studies, because they are generally correlative. Four major challenges identified by Allan (2004) included covariation of natural and anthropogenic landscape features (Richards *et al.* 1996), nonlinearities (Wang *et al.* 2001), incongruence in spatial scale (Hicks *et al.* 1991), and legacy effects (Harding *et al.* 1998). The former two are possible to deal with analytically (Johnson & Gage 1997), but legacy effects (i.e. effects of perturbations in the past that are still evident, but not merely visible) are more difficult to tackle, and probably pose the greatest difficulties in interpreting the results of most watershed-wide studies (Montgomery & Piégay 2003, Allan 2004). Incongruence in spatial scale makes synthesis and interpretation among studies more challenging. However, as the body of literature grows it will be possible to identify in more detail the pathways and mechanisms by which the surrounding landscape at multiple spatial scales influences the stream environment.

Management implications - the watershed approach and brown trout

Brown trout, utilizing small tributary and coastal streams for spawning and rearing (Jonsson *et al.* 2001), probably experience the surrounding watershed to a greater extent than we usually think of, in terms of physical in-stream habitat, water chemistry, and resultant biotic communities (Vannote *et al.* 1980, Gregory *et al.* 1991). Managers in the lower Numedalslågen Basin should prioritize morainal, unconstrained tributary streams where management practices on the stream section level are not constrained by watershed-scale factors. Although the results suggested that marginal riparian logging may enhance fish density (most likely due to increased incident solar radiation), riparian vegetation should be kept even on both sides and scaled according to the upland land cover characteristics to trap excessive nutrients and sediments, which may deter the habitat in the long term (Carignan & Steedman 2000). Therefore, clearcutting in the reach buffer should be avoided. Riparian buffering is most likely to be effective along agricultural-dominated sections of the streams, where young, dense stands of deciduous trees should be provided (Lowrance *et al.* 1985, Myers *et al.* 1985). In-stream habitat management should focus on keeping existing and providing new functional pieces of large woody debris (LWD). A key in that respect is to provide natural inputs of LWD from the riparian zone by retaining at least some large trees (Collins & Montgomery 2002). LWD-pieces should be directly placed along the streambed to back up pebble-sized substrate and create 25 – 44 cm deep pools downstream during summer low-flow. Although morainal streams should be given priority, proper riparian buffering and LWD management may enhance brown trout habitat quality in other types of streams as well, but the overall production may not reach the same levels.

Conclusion

Which factors and combination of factors that related well with the density variation in juvenile brown trout was clearly a function of the spatial scale of the observations. Geology and topography seemed most important at the watershed scale, variability of riparian width in relation to the proportion of the reach buffer which was either logged or under agricultural land use were most important on the reach buffer scale, and pool depth was the most important at the in-stream habitat scale. This suggests that there exist multiple controlling factors (both natural and anthropogenic) over juvenile brown trout abundance across multiple spatial scales in these tributary streams (Frissell *et al.* 1986, Wiens 1989, Armstrong *et al.* 1998). The inherent multivariate nature of such studies makes the underlying mechanisms unclear (Johnson & Gage 1997), but the factors identified in this study are most likely influencing the geomorphology of stream channels and the resultant in-stream habitat quality (Gregory *et al.* 1991, Montgomery 2004). Effective habitat management of anadromous brown trout populations will prioritize morainal watersheds and consider watershed-wide constraints of their summer rearing habitat before initiating fine-scale management actions. Multiscale studies are more likely to arrive at applicable findings for fisheries managers (Fausch *et al.* 2002), and our knowledge is more likely to grow when information-theoretic model selection techniques are employed (Thompson & Lee 2000, 2002, Burnham & Anderson 2002). The focus and findings of this study calls upon a more comprehensive view of streams and their biota by taking into account the influencing factors of the surrounding watershed and riparian zone.

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Appendix 1: Residual density and in-stream habitat characteristics

Note: Residual juvenile brown trout density (i.e. difference between observed density in stream section and predicted density for the stream overall) and in-stream characteristics are given only for fish-bearing stream sections.

Stream	*Section no.*	*Residual density*	*Fine sediments (%)*	*Coarse pebble (%)*	*Depth (m)*	*No. LWD pools (#)*	*% LWD pools (%)*	*Stream width (m)*
Otterstad	1	-0,0722	20	60	0,50	1	25	2,5
Otterstad	4	-0,4722	0	40	0,48	1	33	1,5
Styrmobekken	1	-0,1785	0	50	0,20	1	100	3,0
Styrmobekken	2	0,5715	10	70	0,25	6	100	2,5
Styrmobekken	3	0,4287	0	60	0,25	3	100	2,5
Styrmobekken	4	0,0001	0	30	0,35	3	60	2,0
Styrmobekken	5	0,0715	30	30	0,25	4	100	2,0
Pinnestad	1	-0,2795	35	30	0,27	4	80	4,0
Pinnestad	3	-0,5045	2	50	0,22	3	75	3,0
Pinnestad	4	-0,1545	0	15	0,35	3	60	3,0
Pinnestad	5	0,3455	5	20	0,40	2	67	2,5
Lindsverk	1	-0,0306	0	10	0,25	1	33	3,0
Lindsverk	2	0,2194	0	40	0,40	1	33	2,0
Lindsverk	3	0,6360	0	20	0,35	0	0	3,0
Gavelstad	1	-0,3729	10	25	0,47	0	0	4,0
Gavelstad	2	0,7938	5	20	0,35	1	50	4,0
Gavelstad	4	-0,3729	0	20	0,53	0	0	4,0
Røsholt	2	0,0068	20	50	0,25	2	100	4,0
Røsholt	3	0,2985	0	10	0,43	0	0	7,0
Røsholt	4	-0,2515	0	0	0,25	0	0	4,0
Røsholt	5	-0,3715	0	40	0,50	0	0	4,0
Kringlemyr	2	-0,3158	55	45	0,50	2	50	3,0
Kringlemyr	3	0,2707	30	60	0,35	5	100	2,5
Kringlemyr	4	-0,1543	55	30	0,48	3	100	3,0
Kringlemyr	5	-0,1321	30	20	0,40	3	100	2,0
Haugselva	4	-0,4964	80	20	0,45	2	100	4,0
Haugselva	5	0,4536	70	30	0,35	2	100	4,0
Hvarnesdalen	3	0,2675	25	75	0,25	2	67	2,0
Almedalen	2	-0,2767	95	5	0,35	2	67	4,0
Almedalen	5	0,2733	50	50	0,35	3	75	4,0
Hedrum	4	-0,1449	40	30	0,30	1	100	2,0
Hedrum	5	-0,1211	80	20	0,20	1	25	1,0

Appendix 2: Residual density and reach buffer characteristics

Note: Residual juvenile brown trout density (i.e. difference between observed density in stream section and predicted density for the stream overall) and reach buffer characteristics are given only for fish-bearing stream sections.

Stream	*Section no.*	*Residual density*	*Riparian width (m)*	*Riparian width variability (m)*	*Forested (%)*	*Logged (%)*	*Agricultural fields (%)*	*Grazing fields (%)*	*Imperv. surfaces (%)*
Otterstad	1	-0,0722	10	4	17	0	83	0	0
Otterstad	4	-0,4722	45	35	45	27	10	18	0
Styrmobekken	1	-0,1785	14	2	14	42	0	44	0
Styrmobekken	2	0,5715	38	18	38	22	0	40	0
Styrmobekken	3	0,4287	41	31	42	13	0	45	0
Styrmobekken	4	0,0001	50	50	59	0	0	35	6
Styrmobekken	5	0,0715	6	6	13	87	0	0	0
Pinnestad	1	-0,2795	75	25	75	5	20	0	0
Pinnestad	3	-0,5045	52	48	52	48	0	0	0
Pinnestad	4	-0,1545	100	0	100	0	0	0	0
Pinnestad	5	0,3455	79	29	85	9	6	0	0
Lindsverk	1	-0,0306	50	0	68	0	25	0	7
Lindsverk	2	0,2194	40	20	53	0	39	0	8
Lindsverk	3	0,6360	10	0	21	63	0	10	6
Gavelstad	1	-0,3729	60	0	62	0	38	0	0
Gavelstad	2	0,7938	55	45	57	0	38	0	5
Gavelstad	4	-0,3729	56	42	56	25	19	0	0
Røsholt	2	0,0068	60	40	60	0	40	0	0
Røsholt	3	0,2985	62	38	62	0	38	0	0
Røsholt	4	-0,2515	54	44	54	0	23	23	0
Røsholt	5	-0,3715	35	5	61	10	30	0	0
Kringlemyr	2	-0,3158	70	30	69	30	0	0	1
Kringlemyr	3	0,2707	27	13	27	0	69	0	4
Kringlemyr	4	-0,1543	50	50	50	33	18	0	0
Kringlemyr	5	-0,1321	0	0	12	78	10	0	0
Haugselva	4	-0,4964	19	4	19	12	70	0	0
Haugselva	5	0,4536	65	15	65	10	25	0	0
Hvarnesdalen	3	0,2675	16	4	21	0	40	30	9
Almedalen	2	-0,2767	58	42	78	5	17	0	0
Almedalen	5	0,2733	60	10	59	2	39	0	0
Hedrum	4	-0,1449	23	7	27	0	59	0	14
Hedrum	5	-0,1211	7	3	20	0	61	0	19

Appendix 3: Watershed characteristics

Note: All surficial geology, land cover and land use categories are given as proportion of the watershed draining to the lowermost fish-bearing stream section, whereas “area” is given for the entire watershed. NGU types in parentheses for the surface geological categories.

a) Area, topography, and surficial geology

Stream	*Area (km^2)*	*Gradient (%)*	*Moraine (11, 12, 15)*	*Marine deposits (41, 42, 43)*	*Fluvial deposits (20,50)*	*Weathered- and landslide-derived (70, 71, 72, 80)*	*Peat and bog (90)*	*Bedrock (130)*
Otterstad	2,00	4,95	41,41	7,47	10,84	6,92	0,00	33,36
Styrmobekken	3,75	1,21	14,22	24,12	3,01	6,27	2,12	50,27
Pinnestad	1,89	2,84	53,74	24,83	6,14	0,00	0,62	14,68
Lindsverk	1,29	6,52	59,72	24,95	3,78	0,00	0,00	11,55
Gavelstad	7,00	1,41	57,12	11,07	4,90	0,00	1,50	25,41
Røsholt	17,24	1,05	17,63	12,42	8,68	3,36	5,05	52,85
Kringlemyr	8,12	0,55	7,25	16,87	6,39	0,00	0,34	69,15
Haugselva	22,83	0,30	30,16	3,37	8,98	1,68	3,72	52,09
Hvarnesdalen	2,98	4,42	12,14	2,47	1,67	0,93	4,15	78,64
Almedalen	10,51	0,49	5,77	16,93	3,51	1,91	4,22	61,46
Hedrum	1,50	0,94	0,00	45,98	2,19	0,00	0,77	51,06

b) Land cover and land use

Stream	*Populated*	*Infrastructure*	*Water surfaces*	*Total forest*	*Highly productive forest*	*Agricultural fields*	*Fertilized grazing field*
Otterstad	0,00	0,38	0,01	93,93	49,97	4,52	0,47
Styrmobekken	0,00	0,47	0,26	83,62	28,61	11,78	2,51
Pinnestad	0,00	0,72	0,00	87,96	52,80	10,36	0,37
Lindsverk/Røsbekk	0,00	1,07	0,00	84,52	62,70	12,86	0,07
Gavelstad	0,07	0,68	0,26	90,73	36,30	5,95	0,53
Røsholt	0,10	0,96	0,92	86,22	32,25	8,29	0,70
Kringlemyr	0,03	0,51	0,17	91,32	36,33	4,97	0,62
Haugselva	0,15	0,62	1,34	93,82	45,77	2,77	0,18
Hvarnesdalen	0,09	0,33	1,30	96,00	29,51	0,60	0,00
Almedalen	0,17	0,42	0,24	88,42	37,60	9,02	0,27
Hedrum	0,57	0,89	0,53	71,63	31,83	26,38	0,00