Linking Landscape Characteristics, Streamwater Acidity and Brown Trout (*Salmo trutta*) Distributions in a Boreal Stream Network

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Abstract

Buffam, I. 2007. Linking Landscape Characteristics, Streamwater Acidity and Brown Trout (*Salmo trutta*) Distributions in a Boreal Stream Network.
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Perturbations of stream ecosystems are often mediated by the terrestrial watershed, making the understanding of linkages between watersheds and streams essential. In this thesis I explore the connections between landscape characteristics, streamwater acidity and brown trout (*Salmo trutta*) distributions in Krycklan, a 67 km^2 boreal stream network in northern Sweden. The study focuses on hydrochemical changes during the snowmelt-driven spring flood, a period of episodic acidity which is thought to place a restraint on acid-sensitive biota such as brown trout. pH ranged from 4.5-7.0 at different stream sites during winter baseflow, and declined by 0-2 pH units during spring flood. The magnitude of the pH drop at a given site was in large part controlled by changes in acid neutralizing capacity (ANC) and in natural organic acids associated with dissolved organic carbon (DOC). pH, ANC and DOC were all correlated with landscape characteristics such as proportion of peat wetlands, and stream hydrochemical response during spring flood could be explained by altered hydrological flowpaths through the catchment.

The impact of acidity on brown trout distributions within the stream network was evaluated and compared to the apparent influence of other site and catchment-scale environmental factors. In situ bioassays demonstrated a strong relationship between spring flood pH and juvenile brown trout mortality, with a toxicity threshold at pH 4.8-5.4. In field surveys brown trout were not found at any sites which had pH <5.0 during spring flood, and were rare at sites which had pH <5.5 during spring flood, suggesting limitation by acidity for some streams. However, over the whole of the Krycklan stream network brown trout were more consistently associated with alluvial sediment deposits than with high pH or low inorganic aluminum concentrations. Acidity thus apparently influences trout distributions by setting a maximum potential distribution; within that potential distribution, actual dispersal is influenced by other factors, notably presence of physical substrate suitable for feeding and spawning habitat. Fulfilling chemical thresholds is therefore necessary but not sufficient for sustaining brown trout populations. In the context of environmental monitoring or stream restoration, consideration of physical habitat together with chemical conditions is advised.

Keywords: boreal streams, spatial variability, mesoscale catchments, snowmelt, episodic acidity, pH thresholds, brown trout

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Appendix

Papers I – IV

This doctoral thesis is based on the following papers, which will hereafter be referred to by their respective Roman numerals:

- **I.** Buffam, I., H. Laudon, J. Temnerud, C.-M. Mörth, and K. Bishop. 2007. Landscape-scale variability of acidity and dissolved organic carbon during spring flood in a boreal stream network, *Journal of Geophysical Research* 112: G01022, doi:10.1029/2006JG000218.
- **II.** Buffam, I., H. Laudon, J. Seibert, C.-M. Mörth and K. Bishop. Spatial heterogeneity of the spring flood acid pulse in a boreal stream network. Submitted manuscript.
- **III.** Serrano, I., I. Buffam, D. Palm, E. Brännäs and H. Laudon. Thresholds for survival of brown trout (*Salmo trutta* L.) embryos and juveniles during the spring flood acid pulse in DOC-rich streams. Submitted manuscript.
- **IV.** Buffam, I., I. Serrano, K. Bishop and H. Laudon. Associations of stream water acidity and other environmental factors with the distribution of Brown Trout (*Salmo trutta*) within a mesoscale boreal stream network. Manuscript.

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Background

Streams, watersheds, and scale

Streams and rivers make up less than 0.001% of the water on Earth (la Riviere, 1989), yet are of great significance to ecosystems and society (Carpenter *et al.*, 1992). The health and functioning of flowing water ecosystems is of incalculable value (Naiman, Magnuson & Firth, 1998).

Increasingly, awareness has grown of the connection between stream ecosystems and their terrestrial watersheds. The influence of the terrestrial environment on water quality was already recognized in the early part of the 20th century (Naumann, 1931), and Hynes (1975) encouraged stream ecologists in particular not to consider running waters in isolation: "We must not divorce the stream from its valley in our thoughts at any time. If we do, we lose touch with reality." In the years since then, considerable research effort has been focused on understanding terrestrial-aquatic linkages.

To date, understanding of the terrestrial-aquatic connection has relied primarily on small scale studies, based on individual research plots, hillslopes and very small catchments where detailed measurements can be made. Conversely, most questions about sustainability of water resources and protection of aquatic ecosystems concern the landscape or regional scale. The effects on stream ecosystems due to land use practices such as forestry and agriculture have intensified in many areas, the impact of long-range transport of air pollutants is felt over very large regions, and climate change is a truly global issue. All of these perturbations affect surface water ecosystems over a range of spatial and temporal scales, and are mediated by interactions with the terrestrial landscape, or watershed (Carpenter*, et al.*, 1992; Gergel *et al.*, 2002).

In recent decades, the development of computer-intensive mapping and spatial analysis techniques has widened the opportunities for studying environmental relationships at a range of spatial scales (e.g., Turner, 1989). Stream ecologists and other aquatic scientists have begun to realize the importance of considering patterns and processes at multiple scales (Cooper *et al.*, 1998; Sivapalan, 2003), both in stream ecosystem studies, and notably, in studies of terrestrial-aquatic linkages (Johnson & Gage, 1997; Strayer *et al.*, 2003; Townsend *et al.*, 2003).

Acidification issues: temporal and spatial patterns

Anthropogenic acidification ("acid rain") has been a major environmental concern in many regions, and has focused attention on the connection between surface waters and watersheds. The link between acid deposition, surface water acidification, and loss of fish from surface waters was noted in Scandinavia and North America over 30 years ago (Gorham, 1957; Oden, 1967; Beamish & Harvey, 1972). It was subsequently found that toxicity to fish populations from surface water acidity is mainly due to the effects of increased concentrations of H^+ (i.e., reduced pH) and inorganic aluminum (Al_i) on gill function or structure(reviewed in Gensemer & Playle, 1999). During acidification, aluminum is often leached out of soils and subsequently enters surface waters (Cronan & Schofield, 1979).

There is an important temporal dimension to the relationship between aquatic biota and stream acidity. During acid episodes associated with rain/snowmelt driven high flow events, pH typically decreases coupled with Al_i increase (Wigington *et al.*, 1996). Although chronic acidic conditions represent a sublethal stress to fish and may make them more susceptible to other environmental hazards such as diseases (e.g., Pickering, 1989), it is during acid episodes that many streams reach severely stressful or even toxic levels of pH and/or Al_i. Episodic chemistry is thus generally thought to be an important factor restricting fish distributions in acid-sensitive regions (e.g., Baker & Christensen, 1991; e.g., Degerman & Lingdell, 1993). Since spatial patterns in episode chemistry may be distinct from patterns during baseflow, it is important to consider both periods when designing criteria for the management of aquatic landscapes.

Elucidating the impact of acid deposition on surface waters is not a straightforward task, because changes in water chemistry are dependent on the characteristics of the terrestrial landscape. The type of underlying geology generally dictates the capacity of surface waters to buffer against changes in acidity (e.g., Drever & Hurcomb, 1986; e.g., Cresser *et al.*, 2000). Even in the presence of uniform geology, patchiness in soils, vegetation and land use influence the concentrations of stream solutes controlling acidity (Aitkenhead, Hope & Billett, 1999; Smart *et al.*, 2001; Humborg *et al.*, 2004). Additionally, pH and buffering capacity commonly increase with distance downstream in a given stream network. As a result, monitoring programs which typically focus on large watercourses often omit many of the most acid (and acid-sensitive) streams (Temnerud & Bishop, 2005). This scale phenomenon has in some cases been attributed to shifts in vegetation, soils, and subsurface hydrological flow pathways with distance downstream (Driscoll *et al.*, 1988; Soulsby *et al.*, 2006; Ågren *et al.*, In press), but no clear explanation which applies across all stream systems has been found.

Additionally, the world is naturally acidic, due to the abundance of natural organic matter in the environment (Galloway, 2001). Organic matter contains organic acids which lower the pH of poorly buffered soil and surface waters (Thurman, 1985). In the northern latitudes, soil organic matter breakdown is slow leading to buildup of large pools of organic matter in the form of peat wetlands (Gorham, 1991). As a result, the boreal environment naturally contains much organic acidity. In particular, boreal catchments with high percent wetland commonly provide high concentrations of natural organic acids associated with dissolved organic carbon (DOC) (Hope, Billett & Cresser, 1994; Mulholland, 2003), resulting in acidic surface waters in areas where mineral weathering rates are low (Urban, Bayley & Eisenreich, 1989). In regions which have experienced relatively low levels of acid deposition, these naturally-occurring organic acids frequently play a primary role in controlling the acidity of surface waters (Campbell *et al.*, 1992; Kortelainen & Saukkonen, 1995). In order to fully understand surface water acidification and its potential effects on aquatic biota in boreal streams, spatiotemporal patterns in both natural organic acidity and anthropogenically derived mineral acids must be considered, in addition to the buffering role of geology and soils.

Sampling stream networks

"A continuous view of the river is needed to understand how processes interacting among scales set the context for stream fishes and their habitat." – Fausch et al. (2002)

The study of factors structuring fish populations at the mesoscale (1-100 km^2) are cited as a critical gap in current understanding (Fausch*, et al.*, 2002). For practical issues, direct measurements of stream characteristics with spatially continuous coverage are rare in stream systems larger than headwaters. One of the few studies to attempt this for acidity-relevant chemistry was a survey of Hubbard Brook, New Hampshire, USA which involved water samples taken every 100 m of stream length throughout the entire 40 km^2 catchment (Likens & Buso, 2006). For two snapshots in time, this required several weeks of sampling effort and a total of almost 1400 samples. This study was informative in that it illustrated the very high degree of spatial variability in stream chemistry, particularly in the smallest streams.

Other recent studies have shown promise in relating landscape characteristics to stream water chemistry in mesoscale catchments using a combination of measurements and modeling (Wade *et al.*, 1999; Cooper, Helliwell & Coull, 2004). For instance, Soulsby et al. (2006) found that stream hydrochemistry was related to subcatchment soil characteristics in mesoscale (10-231 km^2) catchments, in much the same way as had been observed for small hillslope/headwater catchment studies. Cooper et al. (2004) were able to model acidity-relevant chemistry at both baseflow and during episodes in streams using relationships between soil type and stream chemistry generated from headwater studies. Evans et al. (2006), utilizing the approach of Cooper et al. (2004), modeled recovery from acidification in terms of potential spatial distribution of acid-sensitive stream biota throughout an entire 256 km^2 catchment.

Scale and management: Brown trout in boreal stream networks

One of the major goals of research on surface water acidification, and of mitigation strategies such as liming, is to help re-establish target organisms, typically fish (Degerman & Appelberg, 1992; Clair & Hindar, 2005). Brown trout, the most common native salmonid in Scandinavian fresh waters, has been the subject of many studies related to acidification (reviewed in Baker & Christensen, 1991). Acidity studies have generally dealt with areas experiencing severe anthropogenic acidification: that is, areas which are both (1) susceptible to acidification due to poorly buffering bedrock and soils, and (2) receiving substantial levels of anthropogenic acidity from the atmosphere (acid rain, acid snow). In streams that have experienced substantial anthropogenic acidification, brown trout distributions are often well correlated with acidity (Andersson & Andersson, 1984; Baker & Christensen, 1991; Degerman & Lingdell, 1993; Hesthagen *et al.*, 1999), suggesting that they are limited by stream chemistry. As a consequence, surface water liming to increase pH has been utilized extensively in Norway and Sweden in the past decades (SEPA, 2002; Clair & Hindar, 2005), with billions of crowns spent by the respective governments to promote stream biodiversity and specific target species such as brown trout.

There is also a large body of knowledge regarding other habitat factors important in controlling trout distributions in non-acidified systems. Brown trout requirements vary with life stage, but are generally related to physical streambed substrate size, water temperature, water velocity, water depth, and physical cover (Elliott, 1981; Mäki-Petäys *et al.*, 1997; Heggenes, Bagliniere & Cunjak, 1999; Armstrong *et al.*, 2003). These physical habitat factors may also be related to spatial variations in the terrestrial landscape (e.g., slope, soil type) or in the near-stream zone (e.g., riparian vegetation, shading). As with stream water chemistry, stream physical habitat important to trout can be related to the larger surrounding watershed; In the Pacific northwest region of the U.S. for instance, geomorphology and hydrology play a major role in structuring salmonid distributions, by influencing the distributions of suitable spawning gravel (Montgomery *et al.*, 1999; Buffington, Montgomery & Greenberg, 2004). Physical stream habitats have also undergone degradation due to human activity. In particular, the straightening of channels for timber floatways associated with intensive forestry has greatly impacted streams and rivers throughout northern Sweden (Törnlund & Östlund, 2002). Physical restoration of streams, commonly used in other regions, has become the subject of much interest in Sweden. Current research seeks to identify ecosystem consequences and predict long-lasting effects of restored channel heterogeneity in northern Swedish watercourses (Lepori *et al.*, 2005; Nilsson *et al.*, 2005).

In order to understand the impacts of human related environmental impacts and effectively address them, we need to understand the relative importance of natural environmental controls on aquatic ecosystems, and of their interactions with one another. This is especially important when assessing the recovery of acidified ecosystems, in which the acidity-related pressure may have relaxed, but biotic responses (e.g., fish distributions) are still patchy. Typically however, the effects of spatial patterns in natural acidity and other habitat characteristics have not been considered together at multiple temporal and spatial scales in the same system. By not considering relevant scales, there is a risk for ineffective or even counterproductive management policies. The purpose of the current study is to add to the limited body of knowledge tying together these issues, using as a case study the Krycklan catchment, a mesoscale boreal catchment in northern Sweden.

Conceptual model

The overarching goal of this study was to examine how spatial patterns in terrestrial landscape characteristics are reflected in spatial patterns in aquatic ecosystems. In order to address this question, I have used a mesoscale boreal stream network with detailed temporal and spatial hydrochemistry data, in combination with surveys of brown trout as a response organism. Spatial and temporal variation in streamwater acidity was focused on, as acidity was hypothesized to be the main factor linking the terrestrial watershed to the distribution of brown trout in the stream network. High levels of acidity are known to be toxic to brown trout, and acidity is known from previous studies to be influenced by landscape characteristics, and to be most acute during periods of high stream flow. Management in the region has focused on acidity as a limitation for fish; the challenge of the current study is to put effects of acidity in the context of other environmental factors. A conceptual model (Figure 1) was first constructed and used to direct individual components of the thesis project.

Addressing acidity dynamics required consideration of both the spatial pattern in the landscape and temporal changes in driving variables. Simplified this can be summarized in the following elements (numbers below reflect the numbered elements in the conceptual model in Figure 1):

1. Spatially, boreal stream networks are superimposed upon a mosaic of landscape elements consisting of patches of different types of underlying geology, soil type, land cover and land use.
2. Temporally, for streamwater chemistry the main driving factor is water flow, which varies over a range of temporal scales and is driven by the amount and timing of precipitation and solar influx.
3. Water flow through the system results in changes in ground water table, with higher flows passing through shallower layers in the soil. The chemical signature of water is influenced by the depth of soil through which it passes on the way to the stream, particularly in the near-stream zone. Temporally variable flow, when convoluted with spatial variation in the landscape, can thus be expected to result in complex spatiotemporal patterns of streamwater chemistry, including acidity.
4. The solutes controlling streamwater acidity and its impacts on fish are acid-neutralizing capacity, or ANC (4a), DOC (4b), and Aluminum (4c), and the most critical time period in the study region is the snowmelt-driven spring flood, an extended period of acidity in many streams. This study focuses on the role of landscape in influencing ANC and DOC during spring flood, while the landscape-Aluminum linkage was covered in a companion study (Cory *et al.*, 2006; Cory, 2006).
5. ANC and DOC combine to control most of the variation in stream pH.
6. Aluminum speciation between toxic (inorganic) and non-toxic (organic) forms is controlled by a variety of chemical factors including pH and DOC (Cory, 2006).
7. Together, pH and inorganic Al impact acid-sensitive organisms like brown trout, with brown trout unable to survive more than a certain threshold of either solute.
8. The spatial distribution of brown trout in the stream network is hypothesized to mirror spatial patterns in acidity during critical periods like the spring flood.

As indicated by the dotted line in Figure 1, landscape characteristics are also expected to influence brown trout distributions in other ways not related to stream acidity. For example, catchment topography and soil types influence the physical character of streambed substrate, which is known to be important for trout habitat. Although not the central focus of this thesis project, other landscape-brown trout linkages will be discussed and compared with acidity-mediated linkages.

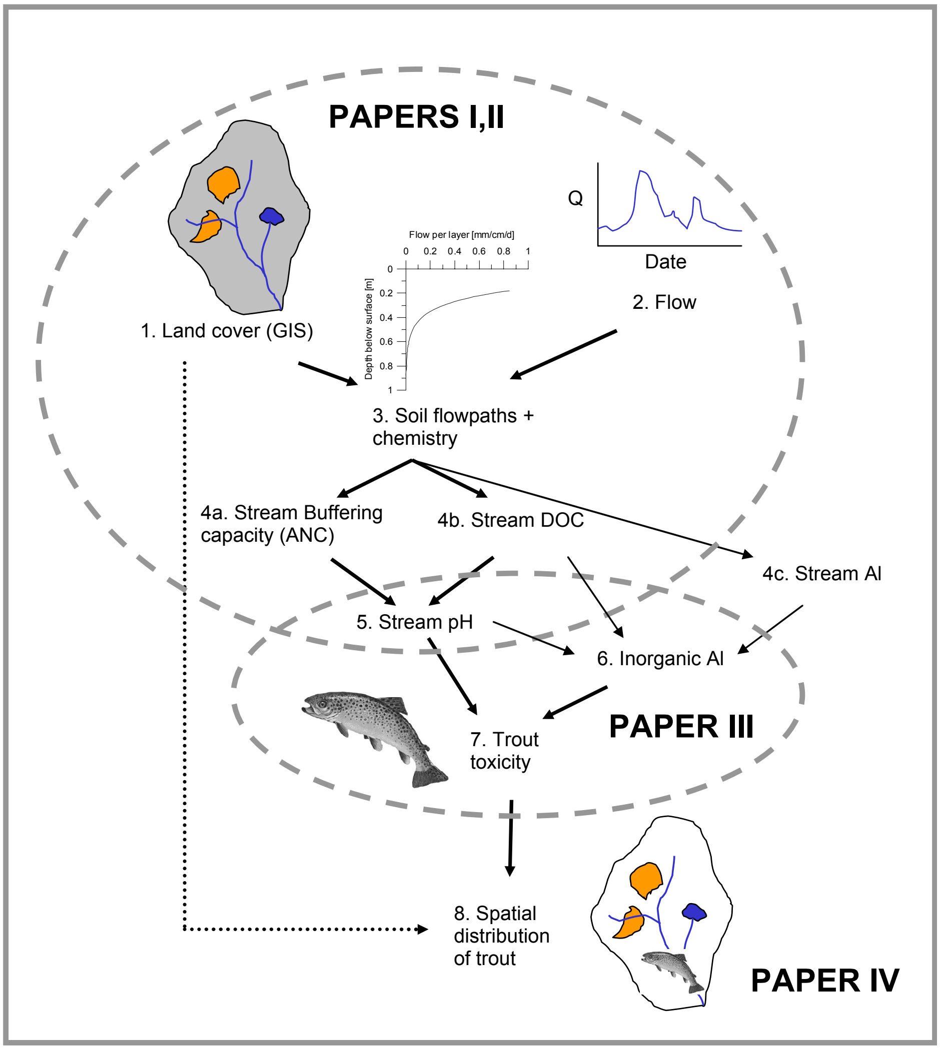

Figure 1. Conceptual diagram of causative linkages between terrestrial catchment characteristics and suitability for brown trout. Dark arrows denote relationships addressed in this thesis, while light arrows denote processes covered in a companion study on Aluminum (Cory*, et al.*, 2006).

Objectives

The four papers in this thesis address different parts of the conceptual model (indicated on Figure 1). The main objectives of the papers are to answer the following questions:

I. What are the characteristic temporal changes in stream water acidity during spring flood associated with major landscape elements (forest, wetland) in a northern Swedish boreal catchment?
II. How do spatial patterns in landscape characteristics influence the spatial distribution of stream water chemistry, with a focus on acidity during the annual spring flood episode?
III. What are acidity (pH, Al_i) thresholds for brown trout eggs and juveniles in naturally acidic boreal streams?
IV. Relative to other environmental factors, how strong are the associations between stream water acidity and brown trout distributions in a naturally acid stream network?

The Krycklan Catchment

Beginning in 2002, the Krycklan Catchment Study (http://ccrew.sek.slu.se/) was developed for site-based research involving scientists and students working across scales from plots to the entire catchment, studying terrestrial-aquatic linkages in the fields of hydrology, biogeochemistry, and ecohydrology. This thesis represents one part of the ongoing work. The study area is the upper 67 km^2 of the Krycklan River catchment in northern Sweden (Figure 2). This catchment includes the Vindeln Experimental Forests, where climate data have been monitored at the Svartberget Research Station (64º 14´ N, 19º 46´ E) since 1980. Annual mean air temperature is 1 ºC with 600 mm annual mean precipitation, of which one-third falls as snow (Ottosson Löfvenius, Kluge & Lundmark, 2003). Snowcover is present for 171 days on average (1980-1999), and spring snowmelt is the dominant hydrological event, exporting up to half of the annual stream flow during a 3-6 week period in April-May. Within the Experimental Forests, soil hydrologic parameters, stream flow and stream chemistry have been monitored in the 50 ha Nyänget subcatchment since 1980 (Bishop, Grip & O'Neill, 1990; Grip & Bishop, 1990). In 2003 an expanded monitoring program was established to study links between spatial and temporal patterns in stream chemistry and biota across a range of spatial scales, from small headwaters/hillslopes up to the mesoscale 67 km^2 Krycklan outlet.

The area currently receives on the order of 2 kg ha^{-1} yr^{-1} each of S (as SO_4^{2-}) and N (as NO_3^-) from atmospheric deposition. Deposition peaked in the 1970's at about 10 kg ha^{-1} yr^{-1} of S, which was less than a quarter of that experienced in southwestern Sweden (Mylona, 1996). Analysis of spring flood episodes in northern Sweden has demonstrated that in this region the pulse of acidity associated with this annual episode is now typically derived primarily from an increase in naturally occurring organic acids in conjunction with the dilution of ANC (buffering capacity), with a smaller contribution from anthropogenically-derived acids (Bishop, Laudon & Köhler, 2000; Laudon, Westling & Bishop, 2000). The anthropogenic component of pH depression was larger when sulfur deposition was higher (Laudon & Hemond, 2002).

The Krycklan study catchment ranges from 126 to 369 meters above sea level (Figure 2A). The area is underlain by gneissic bedrock (Tamm & Malmström, 1926), further classified as svecofennian metasediment, primarily metagreywacke based on current bedrock maps (Geological Survey of Sweden, Uppsala Sweden). In the upper reaches of the catchment, the surficial quaternary deposits are dominated by till varying in thickness up to tens of meters (Ivarsson & Johnsson, 1988). Well-developed iron-podzol soils are common, and organic rich soils are common near stream channels (Bishop *et al.*, 1995). The lower 55% of the catchment is below the highest post-glacial coast line (current altitude 255-260 m in this area), and is influenced by the contribution of coarse-grained glaciofluvial deposits (typically found near the former coast line) and fine-grained silty or sandy sediments which have been deposited in across a large area which was the distal part of a postglacial river delta (Tamm & Malmström, 1926; Ivarsson & Johnsson, 1988). The sediment deposits form a thick layer through which the larger traversing streams have deeply incised channels forming ravines and bluffs of up to 30 m height (Figure 2B).

The catchment is forested primarily with mature Scots Pine *(Pinus sylvestris)* in dry upslope areas and Norway Spruce (*Picea abies*) in wetter, low-lying areas. The forested landscape (Figure 2C) is interspersed with patches of sphagnum-dominated peat wetlands, making up 9% of the catchment area, with up to about 40% coverage in some of the smaller studied subcatchments. Deciduous shrubs and trees, primarily birch (*Betula spp.*) but also alder (*Alnus incana*) and willow (*Salix spp.*), are found in the riparian forest along larger streams (Andersson & Nilsson, 2002). Brown trout *(Salmo trutta)*, Brook trout *(Salvelinus fontinalis)* and Bullhead *(Cottus gobio)* are common in many of the streams.

This is not a "natural system" in the sense of being free from all human impact. Ditching of wetlands (Malmström, 1932; Astrom, Aaltonen & Koivusaari, 2001), a long history of intensive forestry including currently 4% of the catchment clearcut, channelization of larger streams for logrunning (S. Johansson, pers. comm., Törnlund & Östlund, 2002), agriculture and moderate (now low) levels of acid deposition have all undoubtedly had some impact on stream chemistry and biota. But, this is a typical system for the region. Furthermore, these environmental pressures are minor compared to other areas in Sweden and elsewhere which may receive up to 10 times as much acid deposition, and/or have undergone substantial urbanization or agricultural development. There are few inhabitants in the catchment, only 3% agricultural land by area, and <20 km of maintained road length (Figure 2D). Much of the central part of the catchment encompasses the Svartberget Experimental Forests, where timber management has been moderate and well-monitored since the land was handed over to the Swedish Institute for Experimental Forestry in 1923.

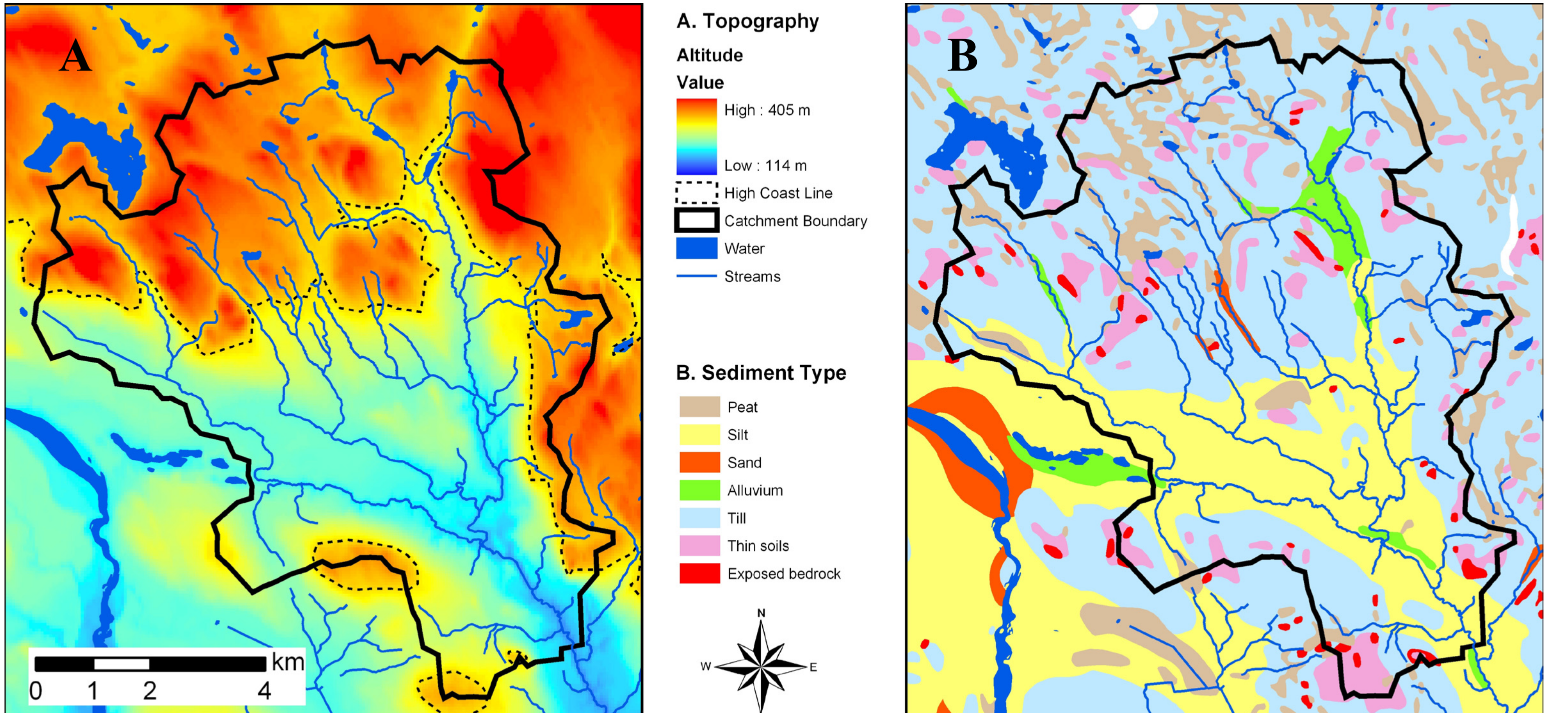

Figure 2. Characteristics of the Krycklan catchment (A) topography including highest former coast line (B) surficial sediment type.

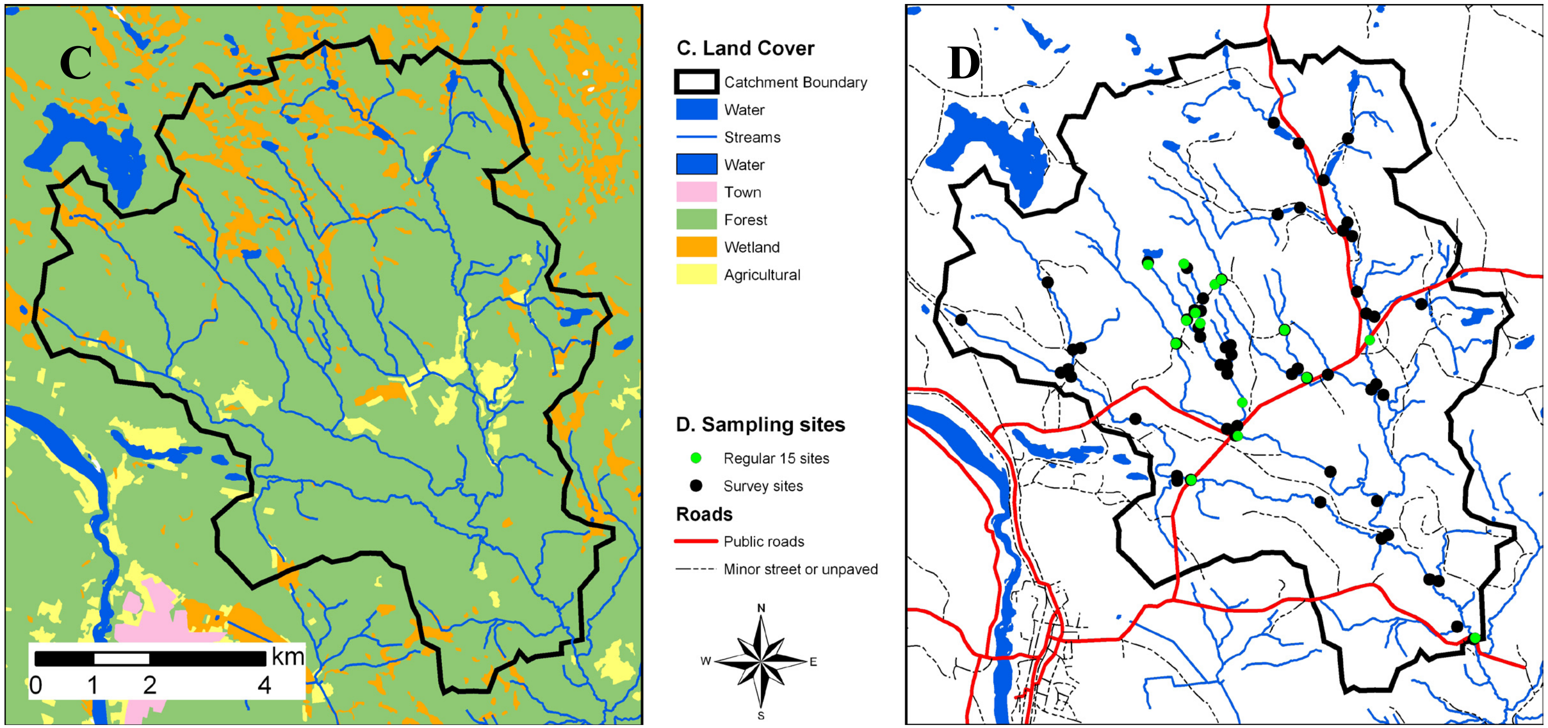

Figure 2, continued. Characteristics of the Krycklan catchment (C) land cover (D) roads and stream sampling site locations.

Methods

General approach

All of the work in this thesis was carried out in the Krycklan catchment (Figure 2). Papers I and II deal with the relationship between landscape characteristics and streamwater chemistry relevant to acidity, with a focus on changes during the spring flood acid pulse. Paper I focuses on temporal changes, using streamwater samples taken every few days during the transition between winter baseflow to spring flood during 2004 in 15 streams ranging in size and land cover type (Figure 2D). Paper II focuses on spatial patterns in the entire stream network, with 67 sites sampled during two snapshot surveys: once during winter baseflow 2005, and once near the peak flow during spring flood 2004 (Figure 2D). Paper III determines the pH and inorganic Al thresholds for brown trout in streams throughout the stream network with in-stream bioassays. For this study, brown trout eggs and 1-year old juveniles were exposed *in situ* to stream chemistry at 9-10 different sites during spring flood in separate experiments (2003 and 2004). Mortality was recorded during the bioassays, and was then related to stream chemical conditions measured during the period of exposure. Finally, paper IV combines information from Papers I-III with the observed distribution of brown trout from an electrofishing survey, to examine the associations between brown trout, streamwater acidity and other environmental factors. Basic descriptions follow of the methods used to determine chemical, catchment and site characteristics, while more detailed descriptions of these and other methods are included in the individual papers.

Chemical analyses and calculations

This work was centered on the causes and consequences of streamwater acidity, so water chemistry was central to the study. During 2003-2005, over 1500 streamwater samples were taken and analyzed for chemistry, and more than half of these were directly used in the studies presented in this thesis. Standard analytical methods were generally used (Table 1). Key parameters used here to describe acidity status are pH, acid neutralizing capacity (ANC), and the concentrations of base cations (BC), strong mineral acids (SAA), dissociated organic acids (OA^-), and inorganic aluminum (Al_i). BC was calculated as the sum of K^+, Mg^{2+}, Na^+ and Ca^{2+} concentrations expressed as μeq L^{-1} of charge, and SAA was calculated as the sum of SO_4^{2-} and Cl^- expressed as μeq L^{-1} of charge. NO_3^- concentrations were too low to contribute substantially to charge balance and were left out of this calculation. ANC describes the ability of ions dissolved in aqueous solution to buffer against changes in pH, and was calculated from the charge balance definition as the difference between strong bases and strong (mineral) acid anions (Munson & Gherini, 1993), expressed here as molar quantities (see also Table 1):

$$ANC = [K^+] + 2[Mg^{2+}] + [Na^+] + 2[Ca^{2+}] - [Cl^-] - 2[SO_4^{2-}] = BC - SAA$$

Table 1. Chemical analyses used in the thesis.

Analyte	Description	Papers	Analytical method	Reference for method
pH	-log $[H^+]$	I - IV	combination electrode (ThermoOrion Ross 8102)	
DOC	Dissolved Organic Carbon	I - IV	Combustion (Shimadzu TOC-V_{PCH})	
OA^-	Dissociated Organic Acids	I - IV	Modeled from DOC and pH	(Hruška *et al.*, 2003)
Ca^{2+}, K^+, Mg^{2+}, Na^+	Major base cations (BC)	I - IV	ICP-OES: Ion-coupled plasma optical emission spectroscopy (Varian Vista Ax Pro)	
Cl^-, SO_4^{2-}, NO_3^-	Major strong acid anions (SAA)	I - IV	IC: Ion chromatography (Dionex DX-300 or DX-320)	
ANC	Acid Neutralizing Capacity	I - IV	Calculated as BC – SAA	(Munson & Gherini, 1993)
F^-	Fluoride Ion	IV	IC	
HCO_3^-	Bicarbonate Ion	IV	Calculated from pCO_2, pH, temperature	(Stumm & Morgan, 1996)
pCO_2	Partial pressure carbon dioxide	IV	Gas chromatography	(Klemedtsson *et al.*, 1997)
Fe	Total Iron	IV	ICP-OES	
Si	Total Silica	IV	ICP-OES	
Al_{tot}	Total Aluminum	II - IV	ICP-OES	
Al_o	Organic Aluminum	III	Ion exchange followed by ICP-OES	(Driscoll, 1984)
Al_i	Inorganic Aluminum (measured)	III	Calculated: Al_{tot} - Al_o	(Driscoll, 1984)
Al_i (WHAM)	Inorganic Aluminum (modeled)	IV	Modeled using the Windermere Humic Acid Model	(Tipping, 1994)

OA^-, including both the strong and weak acid anions, is calculated from DOC and pH using an organic acid model presented by Hruska et al. (2003). The relationship of the major ions (including OA^-) through charge balance equations (Stumm & Morgan, 1996) can be used to model the impact of changes in any given constituent on pH (Köhler, 1999). This principle has been used to describe the relationship between ANC, DOC and pH in papers I and III. In this study we focus on spatiotemporal patterns in ANC, which contributes to buffering against changes in pH; and DOC, which contributes organic acids and thus tends to lower pH. Although rarely occurring in isolation, variation in the major dissolved ions in northern Swedish surface waters can be conceptualized in terms of their effect on changes in pH. In the absence of changes in other dissolved ions, increases in BC (or ANC) will generally be balanced by an increase in pH, while increases in DOC (OA^-) or SAA will generally be balanced by decreases in pH (Laudon, Westling & Bishop, 2000). Bicarbonate (HCO_3^-) also contributes to charge balance in stream waters with pH >5. However, HCO_3^- is non-conservative since it is in equilibrium with CO_2 which can be lost from streamwater by degassing (Dawson *et al.*, 2004), and the role of variation in HCO_3^- was not explicitly considered in this study.

Total aluminum (Al_{tot}) was also measured in papers II, III and IV. For a subset of samples during the time of the in situ bioassays (III), aluminum speciation between organic (Al_o) and inorganic (Al_i) forms was carried out using a modification of the Driscoll-Barnes method (Driscoll, 1984). For use in comparison with actual brown trout distributions (IV), Al_i was calculated from Al_{tot} using the Windermere Humic Acid Model (Tipping, 1994), calibrated as described in Cory (2006).

Catchment characteristics

A range of catchment landscape parameters were examined including catchment area (Papers I and II) land cover type (Papers I and II), catchment soil types (paper II), and the density of major tree species (paper II). This involved two steps: first calculating the catchment area contributing to each given stream sampling site, and then determining the attributes for that catchment. All calculations were based on gridded elevation data (DEM) with a grid resolution of 50 m. A multiple-flow-direction algorithm (Seibert & McGlynn, In press) was used to compute the downslope accumulation of catchment area until the stream network was reached. This defined the local contributing area or local catchment area, i.e., all grid cells draining towards a certain stream cell. Along the stream network all area was routed towards the direction of the steepest gradient. By applying this technique to the contributing area for the 67 km^2 Krycklan catchment outlet, the average of different catchment attributes was calculated for all cells along the stream network. As attributes we used map characteristics including surface sediment type from a 1:100 000 scale digital Quaternary deposits coverage map (Geological Survey of Sweden, Uppsala, Sweden) and land-cover type from a 1:12 500 scale digital land-cover map (Lantmäteriet, Gävle, Sweden). Forest information was estimated from satellite data from the national forest inventory by the k nearest neighbour (kNN) method (Reese *et al.*, 2003). For the sampled stream site subcatchment characteristics were then extracted from the appropriate grid cells along the stream network.

Electrofishing and site characteristics

The electrofishing survey (Paper IV) covered 47 sites distributed throughout the Krycklan network during September 2005, and was accompanied by physical habitat surveys and streamwater chemistry sampling. Electrofishing and habitat surveys used the standard method recommended by the Swedish National Board of Fisheries (Degerman & Sers, 1999). Brown trout were categorized by length as either fry (0+ years old) or parr (1+ year old or older). Habitat factors surveyed included for example assessment of dominant substrate size in the stream bed, dominant underwater vegetation, and dominant riparian vegetation type. An assessment was also made of local sediment type using GIS Analysis (ArcGIS 9.1) of the Quaternary deposits coverage map. Together the local sediment type and physical habitat characteristics were denoted site characteristics, and used for statistical comparison with trout distribution.

Statistical approaches

In the first paper, a descriptive approach was taken to illustrate the different hydrochemical behaviors associated with different catchment types (focusing on wetland vs. forested land cover). The winter baseflow period was compared with the spring flood period in terms of the spatial variability (between-site variation) in different chemical parameters. Paper II utilized a clustering approach (SPSS v 11.0) which separated stream sites into 6 groups based on pH during winter baseflow and spring flood; each group was then described in terms of the distribution of landscape characteristics for the catchments within the group. In paper III, pH thresholds for mortality of juvenile brown trout were determined from bioassay results using a combination of statistical approaches including probit analysis (e.g., Simonin *et al.*, 1993) and lifetime regression analysis (Lawless, 1982). In paper IV, observed trout fry and parr distributions were compared to three groups of factors separately and in combination, using the multivariate Redundancy Analysis (Canoco for Windows 4.54). This analysis describes the amount of the total variance explained in a response variable (in this case density of brown trout parr and fry) by groups of explanatory environmental factors. The three groups of factors examined were (1) stream chemistry, (2) catchment-wide landscape characteristics, and (3) local site characteristics, all as described above.

Results and Discussion

I. Effect of land cover on temporal changes in stream acidity during spring flood

The 15 intensively monitored Krycklan streams spanned three orders of magnitude in size and representing a wide range of wetland cover. Due to the known influence of peat wetlands on stream DOC (Hope, Billett & Cresser, 1994; Mulholland, 2003), streams of wetland dominated catchments were expected to have high contributions of organic acidity (OA^-), and consequently low pH at baseflow, compared to streams of forested catchments. During the spring flood, due to rising water tables forested streams were expected to increase in DOC and OA^-, dilute in ANC and drop in pH, as observed in other recent studies in Swedish boreal streams (Laudon, Westling & Bishop, 2000). It was hypothesized that this change would result in self-similarity between forested and wetland streams during spring flood in the stream chemistry parameters relevant to acidity, i.e. a decrease in the intersite variability of DOC, ANC and pH.

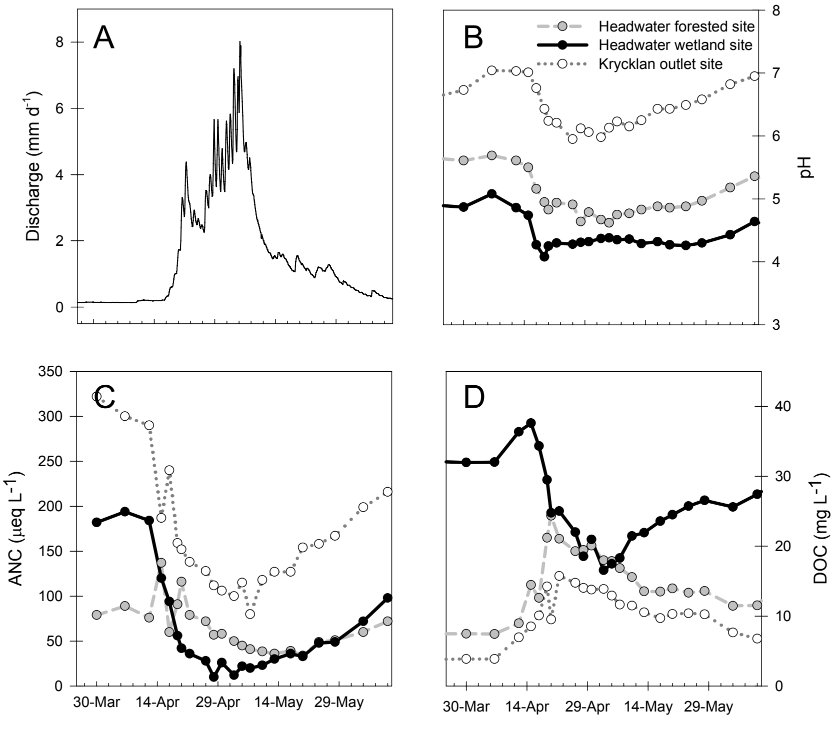

Figure 3. Timecourses of A) discharge at a representative site, B) pH, C) ANC and D) DOC at 3 stream sites representing the extremes of catchment types and hydrochemical behavior during spring flood 2004: a headwater forested site (dashed dark grey), a headwater wetland (solid black), and the 67 km^2 Krycklan catchment outlet (dotted white).

As anticipated, during winter baseflow DOC was positively correlated with subcatchment percent wetland for the 15 study sites, resulting in high spatial variability of DOC and OA^-. BC and ANC also showed clear relationships to landscape characteristics, being highest in streams of large catchments with mostly forest land cover, and lowest at headwater wetland sites. During the snowmelt-driven spring flood which resulted in a nearly 50-fold increase in stream flow, the different sites experienced large and contrasting changes in stream chemistry (Figure 3). DOC and OA^- increased in forested sites and decreased in wetland sites, resulting in reduced spatial variability in their concentrations. BC and SAA were diluted at all sites, resulting in decreased ANC. The sum result of the changes in DOC and ANC during spring flood was that pH dropped at all but the most acidic site, and the dominant acid anion shifted at most sites from SO_4^{2-} during baseflow to OA^- during spring flood. The intersite variability in ANC and pH remained high at spring flood, suggesting that the stream network contained regions of well-buffered waters which could provide areas of refugia for moderately acid-sensitive fish during spring flood.

The basic patterns of changes in stream water chemistry observed during spring flood were consistent with a conceptual model in which hydrologic flow pathway and soil chemistry control stream water chemistry during the transition from baseflow to peak flow conditions. Based on DOC and ANC concentrations, the transition from winter to spring flood stream chemistry could be explained by: (1) a shift from mineral to upper riparian organic soil flowpaths in forested and mixed catchments (Hinton, Schiff & English, 1998; Bishop *et al.*, 2004; Ågren*, et al.*, In press), and (2) dilution of peat water with snowmelt in wetland catchments (Schiff *et al.*, 1998; Laudon, Köhler & Buffam, 2004).

II. Spatial patterns of spring flood acidity and relationship to patterns in landscape

Two detailed snapshot sampling surveys, including 67 stream sampling locations, were used to capture the spatial patterns in streamwater chemistry throughout the stream network during winter baseflow and spring flood (Figure 4). This more spatially complete approach highlighted the importance of soil type and degree of soil sortedness, forest type and age, elevation and catchment area, all of which were correlated with pH behavior. The spatiotemporal variation in pH was related to variation in BC and ANC (positively correlated) as well as DOC and OA^- (negatively correlated). Streamwater pH, BC, ANC and DOC were in turn each related to the landscape characteristics of each individual subcatchment. At spring flood, pH was highest in larger, lower altitude catchments with sorted sediments, and lowest in small, higher altitude catchments underlain by a mixture of peat wetlands and forested till (Figure 4B). The magnitude of the acid pulse varied greatly between sites, from no change to a drop of almost two pH units. The spring flood pH drop was largest in a group of catchments which contained well-developed coniferous forest and an intermediate-high proportion of peat wetlands. Wetland-dominated headwater catchments had low but stable pH. These changes could be attributed to a shift in most sites from deeper flowpaths intersecting mineral soils (at baseflow) to rising flowpaths intersecting organic soil horizons (during spring flood) coupled with influx of new dilute snowmelt.

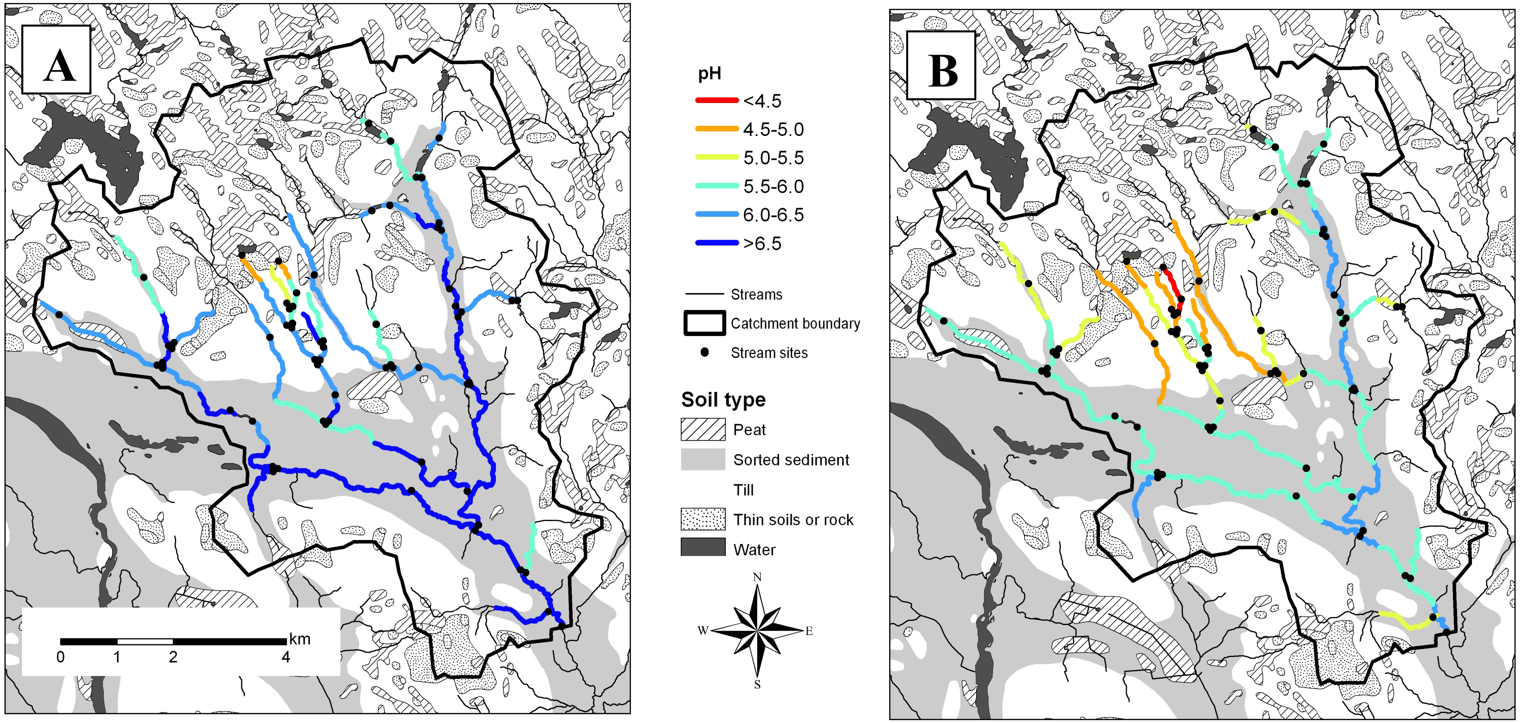

Figure 4. Krycklan catchment, with streams colored by interpolated values of pH to illustrate the spatial distribution of pH at a given point in time for (A) winter baseflow and (B) spring flood. A simplified version of the surficial sediments map is shown in the background.

Increasing pH, BC and ANC with distance downstream, together with decreasing DOC, is a trend commonly found in streams where detailed chemistry measurements have been made (Johnson *et al.*, 1981; Likens & Buso, 2006). In Krycklan, much of the downstream trend in acidity-related parameters is correlated with shifting soil type, from unsorted till in the headwaters to sorted fine sediments in the larger streams. Similar variation in soil type has been linked to changing hydrological subsurface contact time, which then affects stream chemistry (Johnson*, et al.*, 1981; Soulsby*, et al.*, 2006). Well developed coniferous forests, more common in the headwaters in the Krycklan catchment, have acidic organic rich soils which influence the chemistry of water passing through them (Driscoll*, et al.*, 1988; Hongve, 1999).

III. Acidity thresholds for young stages of brown trout in naturally acidic waters

Acidity thresholds for young life stages of brown trout in naturally acidic DOC-rich waters during spring flood were developed by exposing eggs and juveniles in situ at a range of chemical conditions. Toxicity to fish populations from surface water episodic acidity is mainly due to the effects of increased concentrations of H^+ (i.e., reduced pH) on ion balance, and Al_i on gill function or structure (reviewed by Gensemer & Playle, 1999). Most of the previous research documenting acidity thresholds has been carried out in low DOC waters impacted by anthropogenic acidification, which frequently have high concentrations of Al_i. This makes it difficult to separate the effect of pH from that of Al_i, because of co-variation (Baker & Christensen, 1991). DOC-rich streams may provide an exception to this due to the double-edged effect of DOC on acid toxicity: it does lower pH with organic acids, but it also binds aluminum in non-toxic organic forms (Driscoll & Postek, 1996), and thus reduces the effect of aluminum on fish (Witters *et al.*, 1990; Simonin*, et al.*, 1993). Studies in high DOC streams suggest that fish in these systems show greater tolerance to low pH and high Al than fish in low DOC systems (Lacroix, 1989; Laitinen & Valtonen, 1995; Laudon *et al.*, 2005).

In the current study, brown trout eggs and 1-year old juveniles were exposed to stream chemistry in separate experiments. Eggs were buried in small cages at 9 streams distributed throughout the Krycklan catchment just prior to the onset of the spring flood. Survival was recorded after about 10 weeks (typically they had developed to yolk-sac fry by that point). In a second spring flood experiment, 1-year old juvenile brown trout were exposed to in situ conditions at 10 streams, during three separate two-week exposures. The incubations as eggs and as 1-year juveniles were designed to approximate the life stages at which young brown trout are naturally subjected to the sustained period of streamwater acidity associated with the spring flood episode. High mortality of brown trout juveniles occurred during the spring flood at many sites, and was well correlated to pH. Critical thresholds based on probability for mortality during two week exposure were around pH 5.6 (10% probability for mortality), pH 5.2 (40% probability), and 4.8 (80% probability). This is similar to thresholds of pH 4.8-5.4 cited for acidified low DOC surface waters (Baker & Christensen, 1991). No toxic effect could be directly attributed to measured inorganic aluminum concentrations. This could have been due to the difficulty of precisely measuring Al$_i$ in the presence of high DOC concentrations and low Al$_i$, or due to the fact that Al$_i$ concentrations rarely (never in most sites) exceeded the published toxicity thresholds of $>100\ \mu g\ L^{-1}$ (Fivelstad & Leivestad, 1984; Sadler & Lynam, 1987).

In contrast to the juveniles, the eggs and emergent yolk-sac fry had high survival during the spring flood, even at a site with pH as low as 4.0, suggesting that the pH threshold in DOC-rich waters is lower than that of 4.5-5.2 previously established for low DOC systems (Reader *et al.*, 1991; Sayer, Reader & Morris, 1991). The results from this study suggest that in DOC rich boreal streams, first-year juveniles are likely to be the stage most vulnerable to the effects of episodic pH depression associated with the spring flood period.

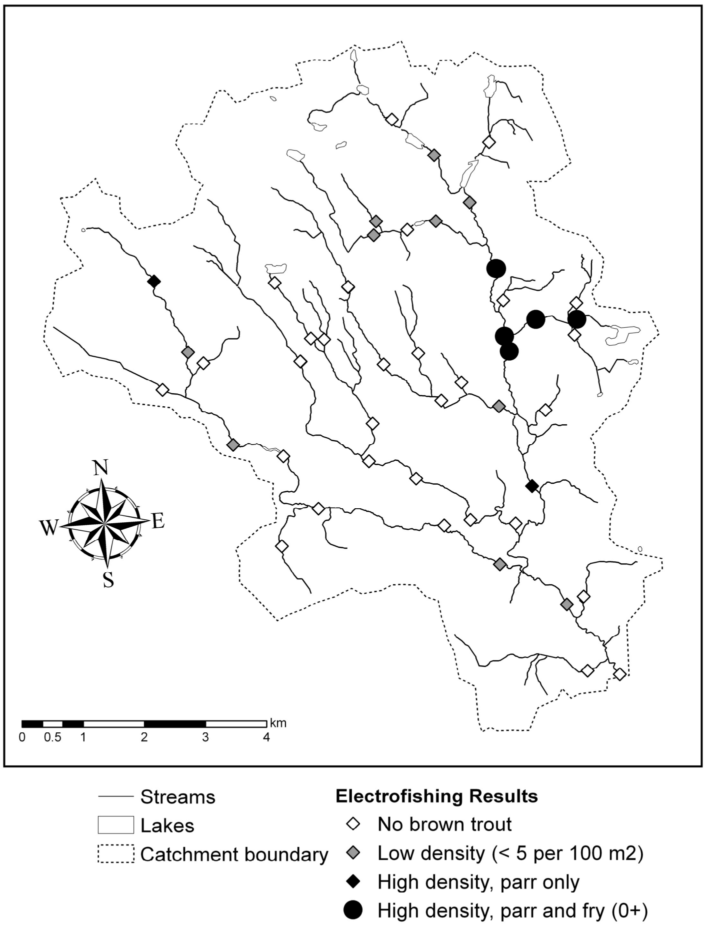

Figure 5. Observed brown trout distribution from electrofishing survey, September 2005 (N = 47 sites). Sites with fry (0+ age trout) are differentiated on the map from those which contained only parr (1+ age and older trout).

IV. Relationship of patterns in brown trout distribution to patterns in landscape, acidity, physical habitat

To explore the role of acidity versus other environmental factors on brown trout distributions in the Krycklan catchment, an electrofishing survey of 47 sites (Figure 5) was compared with the established hydrochemistry data in Paper II, together with stream site and catchment characteristics. In addition, a potential distribution of brown trout based on pH thresholds from Paper III was generated for the Krycklan stream network and then compared with the observed distribution (Figure 5).

The analysis demonstrated that almost the entire measured stream network was suitable for brown trout (pH >5.5) at the time of fishing and during winter baseflow. During spring flood however, the pH drop experienced in most streams resulted in 12 of 47 sites with a pH between 5.0 and 5.5 (limited suitability), and 6 sites with pH below 5.0 (unsuitable for brown trout). Based on interpolation of site measurements to their respective stream segments, during spring flood 20% of the measured stream length in the catchment had limited suitability due to pH, while 18% of the measured stream length was unsuitable (Laudon & Buffam, In press).

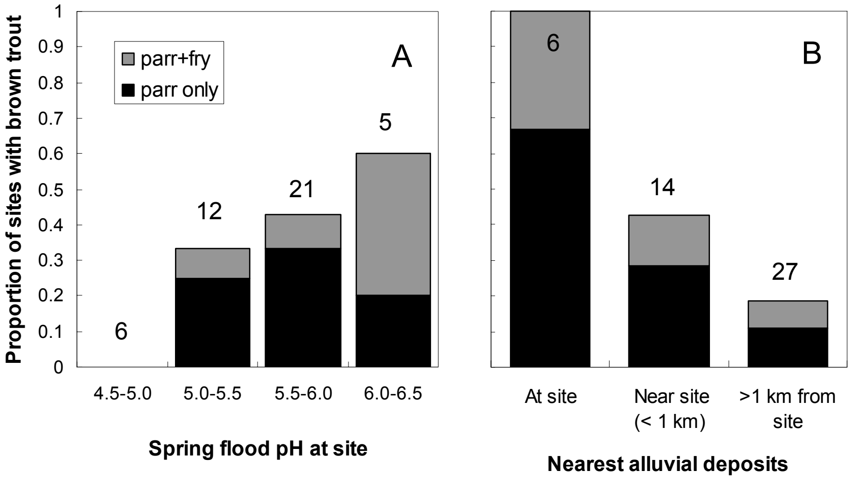

Figure 6. Proportion of sites with brown trout based on (A) pH at the site at time of spring flood or (B) proximity of alluvial sediments along the stream network. The numbers above each bar represent the number of stream sites in the respective category.

Brown trout did appear to exhibit a threshold response: they were not observed at any sites which experienced pH <5.0 during the spring flood episode, and were only rarely found in sites with spring flood pH <5.5 (Figure 6A). However, brown trout distributions were patchy even in less acidic regions of the stream network, suggesting other important environmental factors. In many of the larger streams, trout were rarely found in silty areas in spite of well-buffered chemistry, high pH and low Al_i. Silty areas are not appropriate salmonid spawning habitat because eggs can be smothered (Soulsby *et al.*, 2001; Lapointe *et al.*, 2004), and the lack of physical cover in sites which have only fine sediments may also contribute to the apparent avoidance of these sites by trout.

Based on Multivariate Analysis (Redundancy Analysis), spring flood pH and spring flood Al_i were the chemistry variables most closely correlated with the distribution of brown trout, and together they explained 25% of the variance. Local site characteristics explained 33% of the variance in trout distribution. Brown trout showed an especially strong preference for sites overlying or near alluvial sediments (Figure 6B), most likely indicating the utility of these coarse sorted sediments for spawning and nursery grounds (Heggenes, Bagliniere & Cunjak, 1999; Armstrong*, et al.*, 2003). Whole catchment characteristics explained 43% of the variance in trout distributions. However, the analysis suggested that much of the strong association between catchment characteristics and trout distributions may have been due to effects mediated separately by local site characteristics and stream chemistry

The terrestrial landscape characteristics apparently influenced stream suitability for brown trout at a range of scales (Figure 7). On the scale of whole catchments, the proportions and distributions of major soil types strongly influence DOC and ANC concentrations and their changes during spring flood (Paper I), which in turn influence spring flood pH (Paper II) and potential brown trout distributions (Papers III and IV). On the scale of stream corridors, the distribution of some of the less common landscape elements (lakes and alluvial sediment deposits) were associated with brown trout distributions due presumably to non-acidity related impacts on habitat (Paper IV).

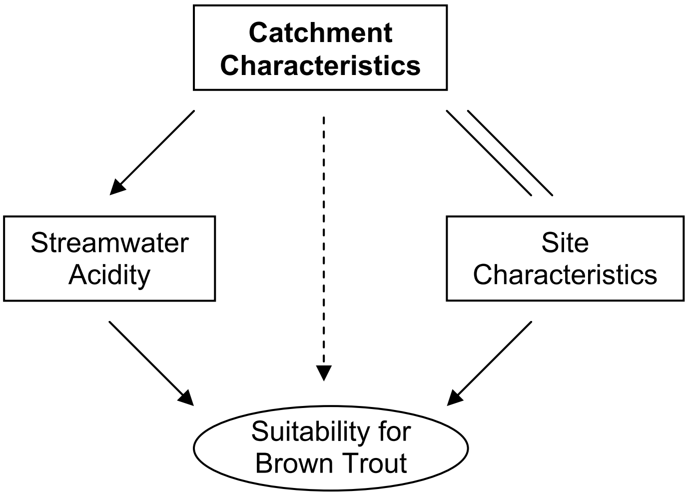

Figure 7. Conceptual diagram with a potential explanation for the strong correlation between catchment characteristics and brown trout distributions. Catchment characteristics influence streamwater acidity, which in turn limits trout distribution. Catchment characteristics are also correlated with site physical characteristics, which in turn influence site suitability for brown trout.

Conclusions and Implications

The conceptual model motivating this thesis is founded on two basic assumptions:

1. the main factors driving patterns in streamwater acidity are spatial patterns in the terrestrial landscape and temporal changes in stream flow
2. the main factor driving brown trout distributions is streamwater acidity

Were these assumptions justified?

Factors driving streamwater acidity

Stream chemistry during the transition from winter baseflow to spring flood was indeed consistent with control by within-catchment soil distributions at the scale of interest. pH was consistently low in headwater wetland streams, and was highest in larger streams with a high proportion of fine sorted sediment soils. Temporal changes associated with the spring flood event also differed depending upon catchment characteristics. pH changed little in headwater wetlands, and dropped the most in small catchments with mixed wetland (peat) and dense coniferous forest cover underlain by till. In large streams with a high proportion of fine sorted sediment soils, pH was well buffered and remained high during spring flood.

Inorganic aluminum (Al_i) is potentially toxic to brown trout and was followed in a companion study in Krycklan (Cory, 2006). Headwater wetland sites had consistently low Al_i concentrations, whereas headwater forested sites on till had the highest Al_i concentrations (Cory, *et al.*, 2006). Concentrations at most sites increased during spring flood, but very rarely entered ranges >100 $\mu g\ L^{-1}$ considered potentially toxic to brown trout (Reader, *et al.*, 1991; Sayer, Reader & Morris, 1991). This was primarily due to the high concentrations of DOC in Krycklan streams, binding Al in non-toxic organic forms. Because pH and Al_i depended upon different landscape factors, the spatial arrangement of some landscape elements (notably, wetland patches) should be considered in studies concerned with acid toxicity. The clear relationship between catchment characteristics and stream water chemistry dynamics during spring flood suggests that a coupled hydrological-landscape model would be a promising research avenue to pursue in the future.

Acidity thresholds

Brown trout acid toxicity thresholds were more clearly related to pH than to Al_i in Krycklan streams. In situ bioassays demonstrated a strong relationship between spring flood pH and juvenile brown trout mortality. Mortality was unlikely (<20% probability) if pH remained above 5.4, but highly likely (>80% probability) if pH dropped below 4.8. Brown trout eggs in contrast showed little sensitivity to pH levels as low as pH 4.0. In situ bioassays exhibited no correlation ($p > 0.05$) between Al_i concentrations and mortality in brown trout eggs or 1-year old juveniles, likely a consequence of relatively low Al_i concentrations.

Factors driving brown trout distributions

In field surveys brown trout parr were not found at any sites which had pH <5.0 during spring flood, and were rare at sites which had pH <5.5 during spring flood (Figure 6). This is suggestive of limitation by acidity, at least in some of the streams. However, covariation of pH with other environmental variables restricts us from fully disentangling limitation related to acidity from the influence other characteristics like physical substrate in the streambed. The spring flood pH threshold values for brown trout in Krycklan were similar to previously published limits for brown trout distribution in acidified streams (Baker & Christensen, 1991; Degerman & Lingdell, 1993). Since the pH experienced during spring flood at a given site is typically similar to that experienced during large rainfall events during summer or autumn, spring flood pH can be thought of as a proxy for a more general episodic pH level (Laudon, pers. comm., Laudon & Bishop, 2002). Thus, the observed correlations with spring flood pH may not indicate that current trout distribution is influenced by the spring flood pH of several months previous, but rather by episodic events which may occur at any time. Winter or autumn baseflow measurements at the same sites in Krycklan gave higher apparent pH thresholds, with for instance no brown trout fry found at sites with pH <6.0 during those periods (compare to Figure 6). This suggests that it is important to take into account seasonal dynamics in acidity when considering suitability of streams for brown trout. Management programs are encouraged to consider episode chemistry in addition to baseflow or average chemistry.

Implicit in the design of this thesis project was the idea that streamwater acidity is a major factor influencing the distribution of brown trout. However, over the whole of the Krycklan stream network brown trout were more consistently associated with alluvial sediment deposits than with high pH or low Al_i. Acidity can thus be envisioned as influencing trout distributions by setting a maximum potential distribution; within that potential distribution, actual dispersal is influenced by other factors, notably presence of suitable physical substrate like the gravel or cobble-sized sorted sediments associated with alluvium, which is used for spawning and nursery habitat (Heggenes, Bagliniere & Cunjak, 1999; Armstrong*, et al.*, 2003). Fulfilling chemical thresholds is therefore necessary but not sufficient for sustaining brown trout populations. As a result, environmental indices based on the absence of species are subject to errors. In the context of environmental monitoring, consideration of physical habitat together with chemical conditions is strongly advised.

Effect of human impacts on watershed-stream linkages

In this study of a low to moderately impacted landscape, a relatively strong correlation (~50% variance explained) was found between basic catchment geomorphological and soil parameters and trout distributions at the mesoscale (1-100 km^2). For future studies, it would be informative to test if these connections were even stronger in a more pristine landscape. That is, the environmental impacts evinced by altered land use, pollution or changing climate may serve to weaken the link between catchment and stream. Regardless, any environmental perturbation should be seen in the context of an already complex pre-existing relationship between terrestrial landscape and stream ecosystem.

Final thoughts and future directions

The approach taken in this thesis is perhaps best seen in the context of the Krycklan Catchment Study as a whole, which is intended to bridge a gap in the understanding between pre-existing small-scale (hillslope, plot-scale) mechanistic process studies, and the much larger scales at which management decisions are typically made. Working at the mesoscale (on the order of 1–100 km^2) has been one of the major advantages, but also one of the major challenges to the research projects outlined in this thesis. The approach also generated many new questions, some of which cannot be answered in Krycklan alone. In particular, we would like to know if the observations made in Krycklan can be applied (1) to other similar boreal regions and (2) across broader regions, i.e., are the relationships general?

To answer these questions requires more advanced process understanding in Krycklan (scaling down), in addition to comparison with other systems (scaling up). As an example of a process-related question which arose: why are brown trout so strongly associated with alluvial sediment stream sites in Krycklan? To answer this question, a number of hypotheses could be tested, including (1) the preference of the alluvial areas for feeding habitat, spawning habitat and nursery habitat (2) the avoidance of areas of fine silt due to lack of cover, lack of food sources, or poor spawning habitat (3) upwelling of well-buffered groundwater in alluvial areas improving local stream water chemistry (4) limited migration of brown trout parr from alluvial nursery habitat. Addressing these hypotheses would require a combination of hydrochemical, observational and fish tracking studies.

Krycklan is not entirely atypical for northern Sweden, but has enough quirks about it to make it clearly unique. This uniqueness, in truth a feature of every catchment, provides both a great opportunity and a difficult challenge in field research. To answer the question of whether the relationships observed are general or not, future research is recommended in testing the conceptual/empirical models generated from Krycklan at other unique sites.

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