Using GIS to Predict Landscape-scale Establishment and Extinctions of Lacustrine Salmonids

Impact from Keystone Species, Exotics, Chemical & Physical Factors

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Cover picture
Schematic connectivity network of lakes within the drainage basin of Nätraån

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Abstract

Spens, J. 2008. *Using GIS to predict landscape-scale establishment and extinctions of lacustrine salmonids: impact from keystone species, exotics, chemical & physical factors.* Doctor's dissertation.
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Understanding the rigorously demanding habitat requirements of salmonids is directly related to the needs of both conservation and management of freshwaters. In this thesis, I used large-scale temporal and spatial data to evaluate which key predictors determine the distribution of self-sustaining lake-living salmonids. Surveys were conducted among more than a thousand lakes in northern Sweden. Multivariate analysis tools were used to model effects of native species, exotics, chemical and physical factors that may govern establishment and extinctions. Historical sources such as archaic lake names, fishers' knowledge and documentary evidence combined with more recent limnological surveys provided estimates and validations of pre-industrial baseline distributions and extinction rates. Among native brown trout (*Salmo trutta*), the extinction rate increased from an insignificant level at pre-industrial times, up to exceeding 3 % lost populations per decade between 1920-2000. Using these data sources, I could also link extinctions to specific detrimental human impact. Long-term impact from introduction of the exotic brook charr (*Salvelinus fontinalis*) was linked to a 10-fold increase of native brown trout extinctions.

Variables from Geographic information system (GIS) data were the best predictors of landscape-scale distributions of the keystone piscivore northern pike (*Esox lucius*), which in turn largely governed salmonid incidence among lakes. Landscape-scale patterns and retrospective whole-lake interventions involving stocking, removal and (re)colonization of pike and salmonids, clearly demonstrated that pike prevented self-sustaining populations of salmonids in these lakes. Set in the context of hierarchical filters, this approach provides a novel, highly predictable explanation to why these northern boreal lakes hold the specific fish communities they do. That is, keystone-specific connectivity is the fundamental determinant that either generates salmonid (low connectivity) or non-salmonid (high connectivity) assemblages and thus dictates fish species community compositions among these lakes. In contrast, water-quality (lakes ranging from highly acid-neutral, clear-murky and ultraoligotrophy-eutrophy) and lake morphometry (ranging from shallow small ponds to larger 53 *m* deep lakes) did not relate well to either salmonid or non-salmonid waters. In conclusion, I recommend that natural connectivity, e.g. S_{Vimax} = maximum stream slope measured in fixed vertical intervals, in drainage networks should be considered as standard characterization of lakes.

Keywords: dispersal barriers, fish community composition, predation, species diversity, historical, abiotic factors, biotic factors, fish passage, fish species distribution, introduced species, lake isolation, local ecological knowledge, migration barriers, natural barriers.

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Till Pappa
“A spirit with a vision is a mission”

Contents

Appendix

Papers I-IV
This thesis is based on the following papers, which will be refereed to by their Roman numerals:
I. Spens, J. 2007. Can historical names and fishers' knowledge help to reconstruct the distribution of fish populations in lakes? Chapter 16 *In* Fishers' Knowledge in Fisheries Science and Management *Edited by* Nigel Haggan, Barbara Neis and Ian Baird. United Nations Educational, Scientific and Cultural Organization (UNESCO), Paris. pp. 329-349.

II. Spens, J., Alanärä, A., and Eriksson, L.-O. 2007. Nonnative brook trout and the demise of native brown trout in northern boreal lakes: stealthy long term patterns? Can. J. Fish. Aquat. Sci. **64**(4): 654-664.

III. Spens, J., Englund, G., and Lundqvist, H. 2007. Network connectivity and dispersal barriers: using geographical information system (GIS) tools to predict landscape scale distribution of a key predator (*Esox lucius*) among lakes. J. Appl. Ecol. **44**(6): 1127–1137.

IV. Spens, J., and Ball, J.P. 2008. Salmonid or non-salmonid lakes: predicting the fate of northern boreal fish communities with hierarchical filters relating to a keystone piscivore. Can. J. Fish. Aquat. Sci. **65**(9): 1945–1955.

Papers, are reproduced with the kind permission of UNESCO (**I**), Blackwell Science (**III**) and NRC Research Press (**II** & **IV**).
Author contributions of articles (**I-IV**): JS conceived the ideas for these studies as well as designed and performed research including analysis of data. JS wrote the first draft of manuscripts. Coauthors assisted JS in editing the final manuscripts (**II-IV**).

Introduction

The ability to determine the past, present and potential distributions of species would facilitate effective management and conservation of many ecosystems. In a holistic approach to freshwater management and conservation, the impact from the main biological, chemical and physical factors that determine the distribution of species need to be assessed (e.g. Allan & Flecker 1993; Jackson et al 2001). Among these factors, it is necessary to distinguish which are human influences on distributions (e.g. Leira et al. 2006), especially those which cause irreversible losses of biodiversity. Currently, most marine and freshwater ecosystems worldwide are being degraded by human impact, and fish species pushed towards extinction (Harrison & Stiassny 1999; Pitcher, 2001). Here, reconstructions of historical distributions of local populations, i.e. baselines, are essential for monitoring future changes, and for rebuilding natural ecosystems. Thus, knowledge about basic questions as which populations have survived and which have been lost is fundamental for practical conservation and management. Integrating the use of wider temporal and spatial scale studies in ecology would enable investigations to move from current brief snapshots at a local scale to the context of the wider landscape and to incorporate the historical dimension, e.g. "before and after" human impact. Specifically, I suggest that wider scale empirical studies including an essential baseline historical scale (e.g. pre-industrial), and wide spatial scales (e.g. landscape-scale involving thousands of lakes) in the context of entire drainage networks, may be needed for statistical assessment of local extinctions. In contrast, the accumulating evidence from the many single lake and isolated small-scale studies ("garden experiments") in freshwater ecology are inherently inadequate for capturing essential large-scale patterns (Jackson et al. 2001). However, large-scale field surveys are time-consuming with both logistic and financial difficulties involved. But with the rise of new statistical techniques, geographical information system (GIS) tools and electronic access to databases with species occurrences, the development of predictive distribution models in ecology is increasing rapidly (Guisan & Zimmermann 2000; Ferrier & Guisan 2006).

Parameters easily extracted from historical and current topographic maps should enable larger-scale studies of variations in time and space to be undertaken with significantly less effort. Several previous studies identify that physical factors like lake isolation (as derived from maps) is associated with fish community composition (Robinson & Tonn 1989; Tonn et al. 1990; Olden et al. 2001). I expect that relevant measures of map-derived connectivity will increase our ability to accurately describe past and present distributions of freshwater species and potentially to predict the extent of their future invasions. A promising tool for predicting species' distributions, is the use of series of hierarchical filters , e.g. connectivity, chemicophysical factors and coexistence-rules, which a species must pass to be present in a given location (Tonn et al. 1990; Poff 1997; Quist et al. 2005). One feasible way to construct this filtering framework may be to focus on taxa that are strong interactors, i.e. "keystone species" (Poff 1997) like some predators or competitors. The widely tolerant northern pike (*Esox lucius*) and more sensitive salmonids have previously been classified as a keystone species (e.g. Power et al. 1996; Hershey et al. 1999). Furthermore, salmonids are shown to be highly sensitive to exotics (e.g. Nilsson 1985; Levin et al. 2002), physical (e.g. barriers: Novinger & Rahel 2003; siltation: Witzel & MacCrimmon 1983) and chemical factors (e.g. acidity: Bulger et al. 1993; eutrophication: Igoe et al. 2003). Since salmonids are rigorously more demanding than many other fish species, they have been suggested to be effective indicators of ecosystem health (Maitland et al. 1981). They suggest that by protecting wild salmonids, most other cohabiting species are also automatically preserved, while other considered species do not serve as well as indicators. Furthermore, Maitland et al. (1981), stress the need to balance economic values with longer-term cultural, social, and natural values and that fisheries workers should consider the great potential of involving the public as "watchdogs" for salmonids. Salmonids are also among the most pursued freshwater species by anglers , e.g. in 2001, 37.5% of all freshwater anglers in the U.S.A. sought salmonids (Leonard 2005). Consequently, they are of vital importance as a leisure resource and considered to be catalysts for economic growth (Leonard 2005). Thus, the ability to determine the historical, present and potential distribution of salmonids and understanding the main factors that govern them, is directly related to the needs of both conservation and management of freshwaters.

GIS-derived models appear, particularly from a logistic standpoint, to be the fundamental framework to use, to start revealing ecological crossword-puzzles of species distributions in watersheds, identifying the "predictable pixels" of landscape biodiversity. Therefore, I anticipate that a holistic approach which incorporates GIS-derived models with large temporal and spatial scales as well as data relating to the main biological, chemical and physical factors that determine salmonid distribution, will be essential for future understanding, research, management and conservation of entire drainage networks.

Thesis objectives

This thesis is part of a long-term conservation and restoration effort with focus on lacustrine salmonids. My initial aim is to reveal and validate with multiple sources and methods, historical baselines and current landscape-scale distribution of salmonids among thousands of lakes in a northern boreal landscape. The objective of this thesis is to answer the following questions:

1. What are the current and historical distribution patterns and how far back in time can we determine baselines? (Paper **I**-**IV**)
2. Is it possible to construct and validate effective GIS-models for predicting landscape-scale distribution
    - at the species level, exemplified with a keystone species, (Paper **III**)
    - and at the community level, exemplified with salmonid and non-salmonid communities? (Paper **IV**)
3. How important is the natural/human impact from
    - physical factors, (Paper **II**-**IV**)
    - chemical factors, (Paper **II**-**IV**)
    - exotic and native species, (Paper **II**)
    - keystone species (Paper **IV**)

for the distribution and survival of salmonid populations?

Study areas

This thesis includes data from lakes (n = 1 563) and connected streams situated within watersheds covering 7 650 *km2*, centered near 63°36´N 18°10´E in the northern boreal region of Sweden. The lake district is a result of deglaciation 9 600 years ago and subsequent isostatic rebound (currently 8 mm year^{-1}) of the land from the sea. Papers (**I**-**IV**) together include a total of 37 complete (Moälven, Nätraån, Husån, Idbyån, Näskeån, Strömsån, Banafjälsån, Saluån, Utbyån, Flärkån, Fanbybäcken, Dombäcksbäcken, Skravelbäcken, Burebäcken, 25 smaller coastal drainages that included less than 5 lakes each) and 6 partial river drainage basins (e.g. Ångermanälven, Gideälven, Lögdeälven, Dockstaån), each terminating independently in the Baltic Sea (Fig. 1).

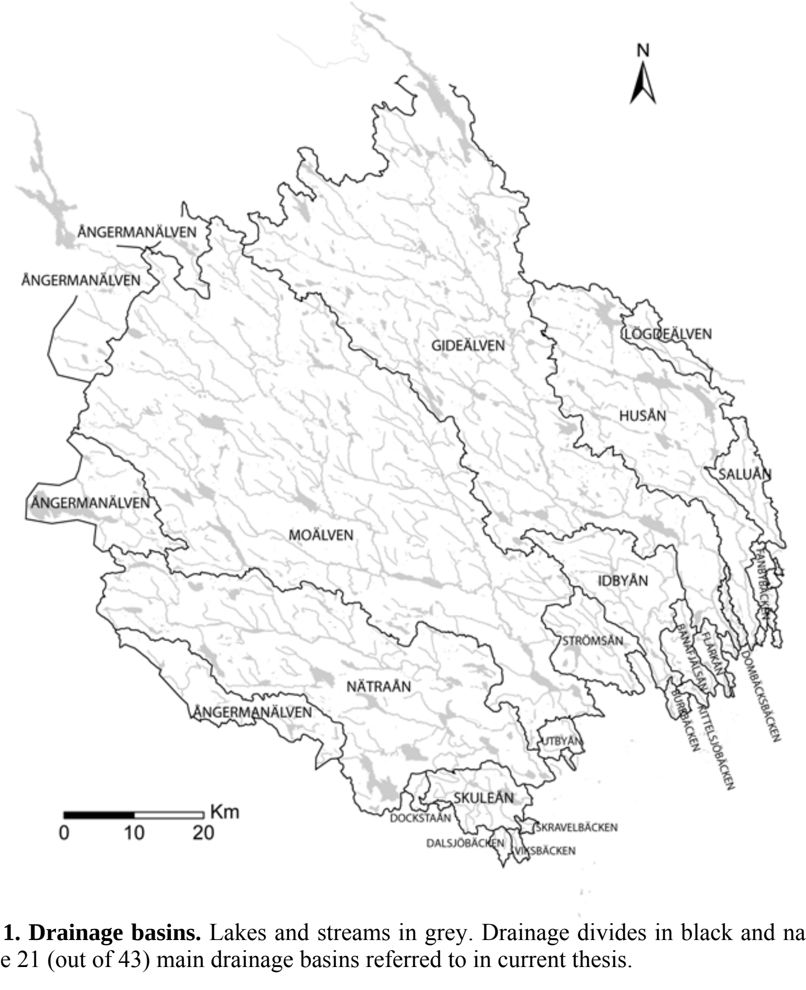

Fig. 1. Drainage basins. Lakes and streams in grey. Drainage divides in black and names of the 21 (out of 43) main drainage basins referred to in current thesis.

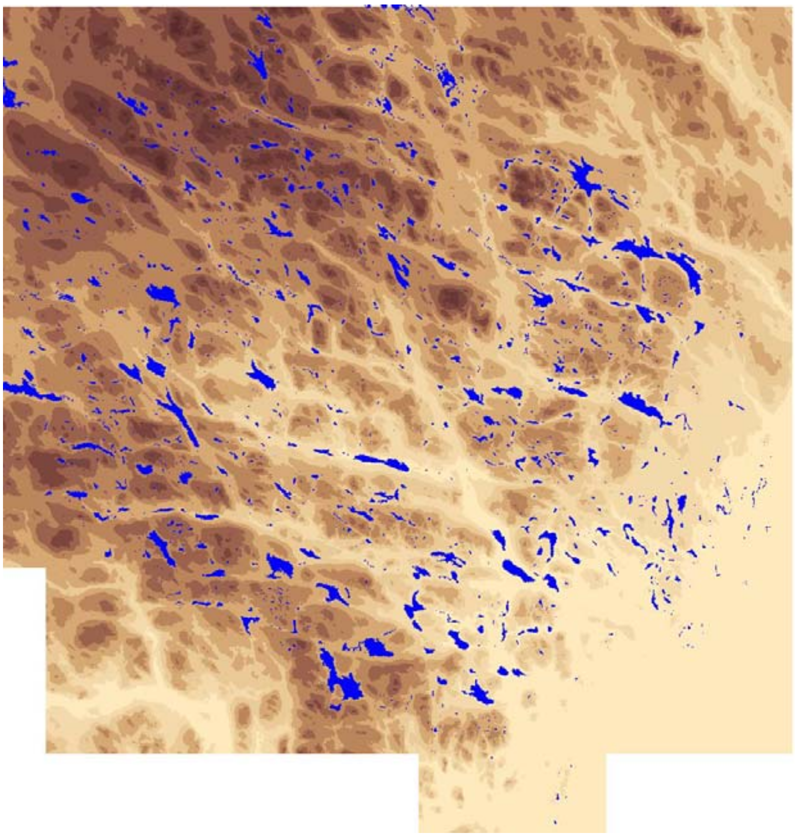

Fig. 2. Topography of the study areas. Lakes in blue. Altitude in graduated colour from light beige (sea-level) to darkest brown (>500 *m* above sea line).

Mean annual air temperature (1921-2005) was 0 °*C* at 500 *m* altitude, to 3 °C at sea-level (SMHI 2006). Mean annual precipitation (1961-1990) ranged from 500-700 *mm* (SMHI 2008). A continuous icecover is normally present from October-November until April-May. The drainage basins range from 0 - 650 *m* above sea level, and studied lakes are located 0.1 – 515 *m* above sea level (Fig. 2). The landscapes range from coastal to inland, including hilly as well as flatter productive forest land, to low slope agricultural areas and wetlands. On average, sphagnum-dominated peat wetlands make up 11 % of drainage basins, and many of the smaller lakes are surrounded by peat. Lakes range from clear to dystrophic, and mostly oligotrophic to mesotrophic, although there are several eutrophic lakes in areas with agriculture. The region is sparsely populated, averaging eight inhabitants per km^2, primarily concentrated in a few population centers. Most lakes (99%) are situated within 5 *km* from present or historical human settlements. Merely 2 % of lakes were being regulated for hydropower (n=18) or for other usage (n=15).

In these drainage basins, the lake fish fauna (27 species) was generally dominated by “coarse” fish communities: perch (*Perca fluviatilis*), Northern pike, roach (*Rutilus rutilus*), burbot (*Lota lota*); occasionally with bream (*Abramis brama*), bleak (*Alburnus alburnus*), dace (*Leuciscus leuciscus*), ide (*Leuciscus* *idus*), bullhead (*Cottus gobio*), whitefish (*Coregonus* spp.). Salmonid lake communities included brown trout (*Salmo trutta*) and/or brook charr (*Salvelinus fontinalis*) exotic, and/or occasionally Arctic charr (*Salvelinus alpinus*) which is mainly introduced. Perch or roach often occurred with salmonids. Grayling (*Thymallus thymallus*) and rainbow trout (*Oncorhynchus mykiss*), an exotic, were only rarely established in lakes. Atlantic salmon (*Salmo salar*) was not established in any lakes although may occur seasonally in "transit lakes". The glacial relicts, vendace (*Coregonus albula*) and smelt (*Osmerus eperlanus*), were typically found below the highest coastline. Pike-perch (*Stizostedion lucioperca*) was restricted to a few of the largest lakes in the lower parts of drainages. Crucian carp (*Carassius carassius*), three-spined stickleback (*Gasterosteus aculeatus*), nine-spined stickleback (*Pungitius pungitius*), rudd (*Scardinius eryhtropthalmus*) and ruffe (*Gymnocephalus cernuus*) were occasionally found in lakes, among both salmonid and "coarse" fish communities. Other sporadically occurring species were eel (*Anguilla anguilla*), tench (*Tinca tinca*) (non-native) and minnow (*Phoxinus phoxinus*). Brook lamprey (*Lampetra planeri*) and river lamprey (*Lampetra fluviatilis*) were only found in running waters, but river lamprey did migrate through several "transit" lakes.

Studied lakes and geographic extent in respective paper:

- Paper **I**: Study included 1 509 lakes with special focus on native brown trout lakes, minimum 0.5 ha.
- Paper **II**: Study included all lakes with native or translocated brown trout (n=193), and excluded those lakes with introduced pike.
- Paper **III**: Study included 1 365 lakes, minimum 0.5 ha.
- Paper **IV**: Study included all salmonid and pike lakes (n=1 029) that I found within all drainage basins (7 650 km^2). The Ångermanälven drainage basin and many smaller coastal basins, not included in **III,** was included in this study. Lakes without salmonids or pike were not included (excluded lakes mainly fit in the smallest size class < 1 ha).

Methods and Data sources

Landscape-Scale Distribution of fish

Prior to the collection of data assembled in the LIMNOR database (**I**) and the undertaking of studies for this thesis (papers **I**-**IV**), there were little (if any) data readily available for researchers, managers or conservationists concerning the historical and current fish species distribution in this studied landscape. I extracted baseline distribution of fishes from historical sources (historical maps Fig. 3, archives Fig. 4 and interviews). Although when evaluating recent anthropogenic impact (e.g. rotenone) carried out between 1984-2006, I was generally able to generate baseline data by testfishing. Current distribution of fishes was extracted by testfishing methods (papers **I**-**IV**: survey nets, regular nets, trapping, trawl, rotenone, electrofishing and angling) questionnaires and interviews. Abundance data were generally collected with survey nets and electrofishing and converted to presence-absence for these studies. Presence-absence data is less prone to impacts of ordinary cyclic environmental change (e.g. daily, seasonal or annual variation) than abundance data, and facilitates comparison of data collected using different methods and sources as well as reduces the risk of over-interpretation in lake fish community studies (Jackson & Harvey 1997). The fundament of long-term sustainability of biodiversity is essentially the continued existence of self-sustainable populations. So in order to determine the fundaments that will have an overriding long-term importance to conservation and management, I focused on the presence-absence of self-sustaining fish-species, assessing introductions, establishment and extinctions in particular.

Historical introductions

I collected 6 480 records with stocking events of 26 fish species during the years 1868-2006. Historic documents from three major forest companies, county and municipality administrations, Fishery management organizations (FMOs), the National Board of Fisheries and other sources were used. I supplemented archival data with stocking data that I collected in face-to-face interviews carried out between 1984-2006, among FMOs and others responsible for both legal as well as illegal introductions. For quality control, stocking records and matching presence records of the exotic species brook charr in all lakes was used to attain a minimum estimate of omissions in the total database. In this search for potentially overlooked stocking events among all lakes within the study area, I identified just one half percent of lakes with brook charr resulting from undocumented brook charr introductions.

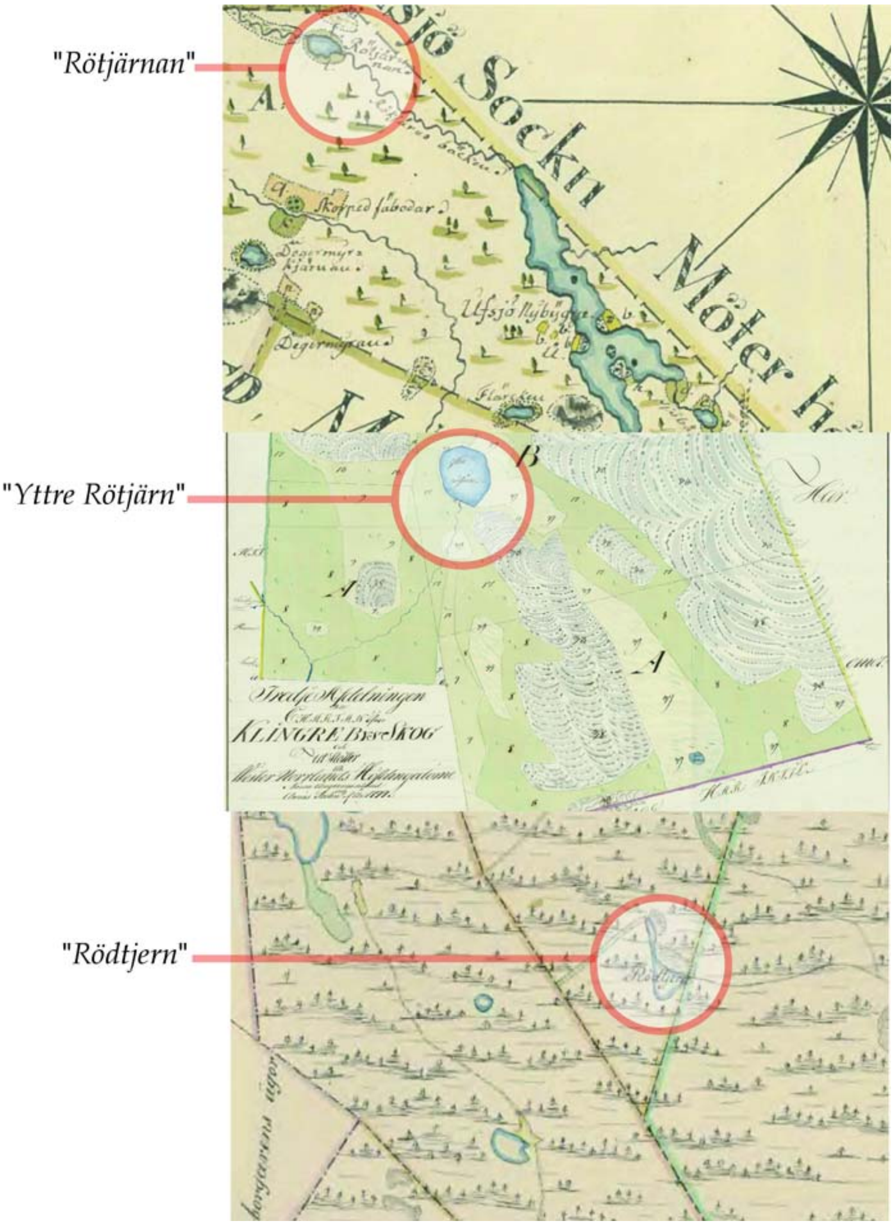

Fig. 3. Three examples of historical maps (dated 1772, 1799 and 1844 respectively). Small parts of local maps within the study area “socken- och skifteskartor” (Swedish) archived at The Swedish National Land Survey. Highlighted lakes with Rö-prefixes, an archaic term for brown trout. 92% of all lakes with Rö- or other dialectal terms (e.g. Stenbit- or Lax-) commonly used for brown trout included in their historical lake names had native brown trout populations. The oldest map I found with Rö-prefixes was dated 1672.

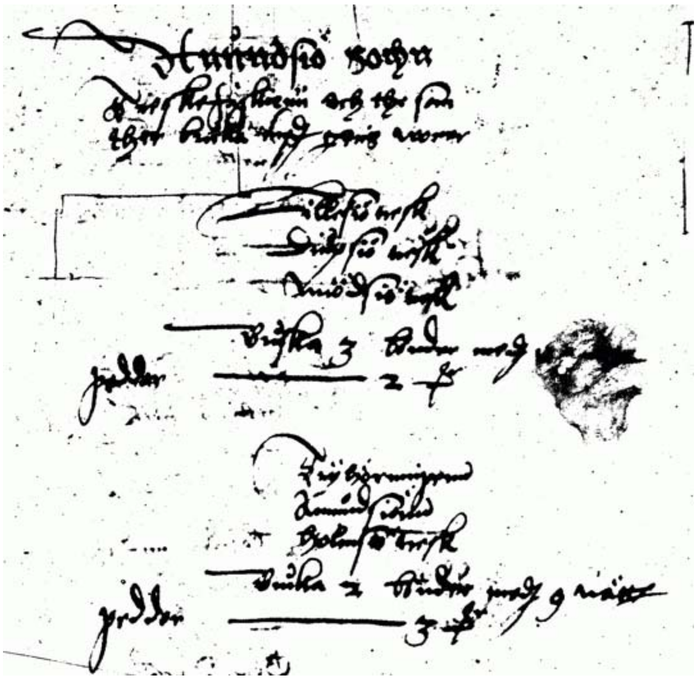

Fig. 4. Taxation record from the year 1565. Example from the parish of Anundsjö, naming six small lakes belonging to the Galasjöå-drainage and quantities of pike (gädda in Swedish, in list: first word left margin in 8th row & last row).

Chemical factors

Water chemistry

I collected 19 473 records of water chemistry data measured at multiple sites in 267 streams and 790 lakes, from different sources, mainly from municipalities and SLU. Each record normally included measurements with standard analytical methods: pH, alkalinity, conductivity and water color. Nearly half of all records also included total phosphorous. The whole dataset (1968-2006) was collected to obtain a general overview of the individual variation of lakes and streams and their seasonal variation. However, for statistical analysis, I only selected those records that were sampled in the lake centre under ice with a Ruttner-sampler at two meters depth during stable winter conditions. I chose these consistent samplings during the stability of winter conditions to minimize impacts of ordinary cyclic change (e.g. episodes or annual variation)[1]. Mean values were calculated for those

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[1] Additional motive to winter baseflow sampling: While baseflow chemistry is often consistent during decades in these lakes, samples taken during flood episodes and linked lowest pH may vary considerably in time and scale. So even with several samples from a single episode (with considerable costs and logistic difficulties involved), it may be difficult to determine how far the sampled pH is from the lowest value in that particular episode. With these baseflow measurements in lakes, I capture the chemistry that fish are exposed to during most of the year as well as provide a useful correlate with lowest pH recorded during episodes. Fortunately, baseflow water chemistry is closely related to the magnitude of spring flood acidity pulses (ANOVA: $R^2 = 0.56$, $P < 0.001$, estimate from episodes in 53 lake outlets in current database; ANOVA: $R^2 = 0.43$; $P < 0.001$, estimate from 22 episodes in 11 streams listed in Table 2 in Laudon et al. 2000).

lakes sampled in multiple years, and for limed lakes only pre-liming data were used. I recorded timing and dosage of lime for 183 lakes (2 010 liming events) from state liming program data and unofficial data (n = 30 lakes) collected from FMOs. I also calculated the extent of potentially affected lakes situated downstream liming sites. For more details on water chemistry methods, see papers (**II-IV**).

Rotenone

Historical records from major forest companies, county and municipality administrations and FMOs concerning rotenone usage revealed that systematic eradication of fish communities by means of rotenone had been carried out in 179 lakes within the study area during the years 1956-1995 (Fig. 5). I interviewed field personnel and a manager responsible for carrying out many of the historic rotenone treatments and followed those rotenone treatments carried out during the latter years (1986-1995). These retrospective whole-lake experiments gave me the opportunity to evaluate long term recolonization of fish populations in lakes treated with rotenone. The regularly applied dosage in lakes was 0.5 *mg* rotenone L^{-1}, with one exception where 1.5 $mg\ L^{-1}$ was applied to kill off crucian carp.

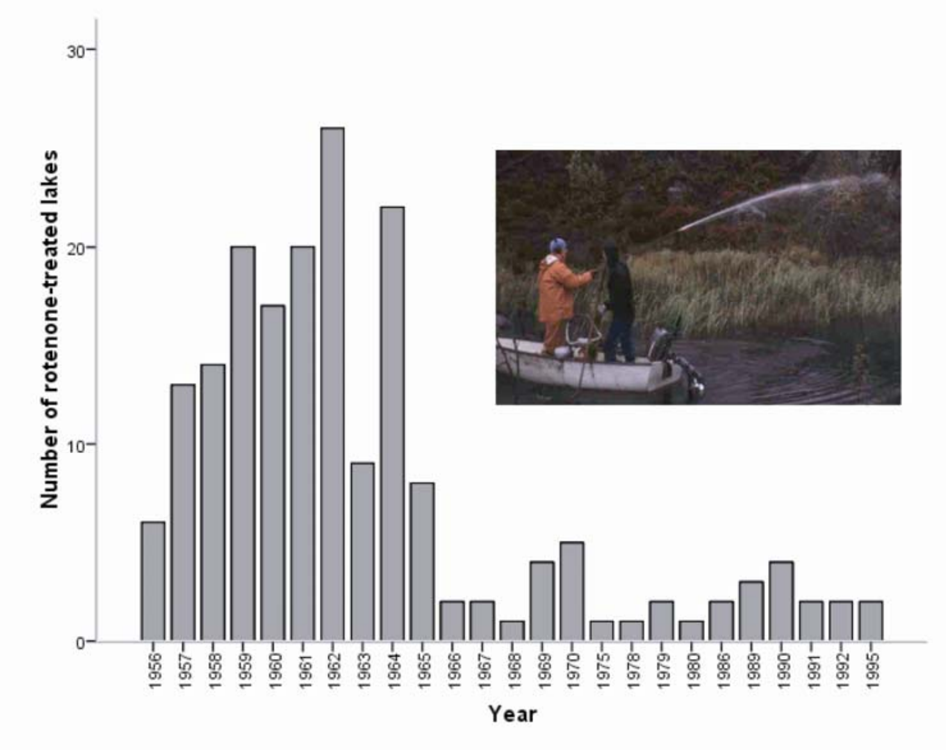

Fig. 5. Number of rotenone-treated lakes within the study area. Lakes were treated during the forty-year period 1956-1995.

Physical factors

Morphometry

Volumes, maximum and mean depths of lakes were determined by measurements with echo sounder from boat or sounding line from ice. Equidistances of 1 or 2 meters were normally used, although up to 5 meters equidistance was used for larger lakes (> 500 ha). Lake volumes (n = 423) were estimated planimetrically from bathymetric charts (chart example in Fig. 6). I determined specific lake shapes from relative hypsographic curves in order to choose the optimal volume calculation formula for each individual lake. Subsequently, I used the formula $V = \sum_{i=0}^{n} \frac{E}{3}(A_i + A_{i+1} + \sqrt{A \bullet A_{i+1}}$ calculating volumes of lakes with convex shapes and $V = \sum_{i=0}^{n} \frac{E}{2}(A_i + A_{i+1})$ for linear and concave shapes, where E = equidistance and A = area limited by the contour line of E_i (Hutchinson 1975; Bain & Stevenson 1999).

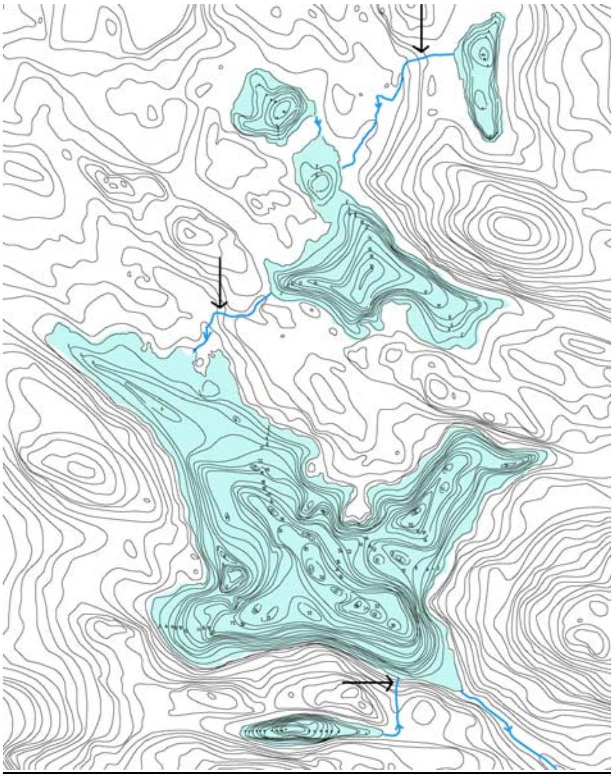

Fig. 6. GIS-layers with water bodies, lake depth contours and land elevation contours. Is it more efficient to study land contours than lake depth contours in order to predict fish communities? Black arrows point to barriers (S_{V5max} > 6.6; Table 1 & paper **III-IV**) that separate four very different (only one shared fish-species among two lakes) fish community assemblages from one another. Distance to nearest neighbouring lake merely ranges from 50 *m* to 0.5 *km*. The map is modified from bathymetric maps archived at the Municipality of Örnsköldsvik.

Anthropogenic barriers

Man-made barriers to fish migration up- and downstream from all salmonid lakes were identified to determine the access to spawning-habitats as well as the progeny's ability to return to the lake. I also identified manmade barriers up- and downstream lakes treated with rotenone, and many other lakes. Several types of constructed barriers were identified, e.g. dams, floatways, culverts and wire nets (Fig. 7).

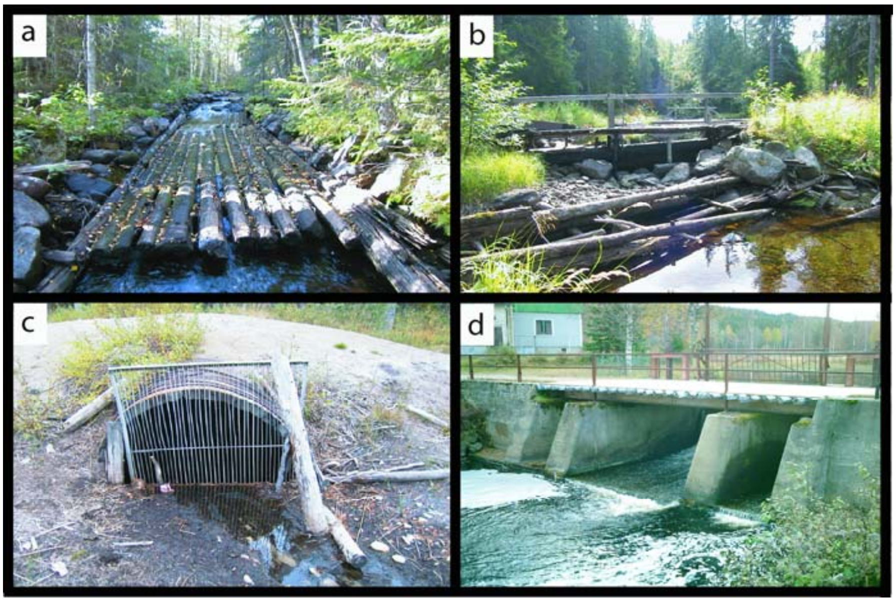

Fig. 7. Examples of anthropogenic fish-migration barriers with potentially critical effects on species distribution. a) Timber floatways in the stream Knäsjöbäcken may contribute to prevent pike from reinvading a series of rotenoned lakes situated upstream with introduced salmonids. b) The Galasjöå-drainage directly upstream this dam contain only exotic salmonids while directly downstream is dominated by native salmonids. c) Barred culvert completely stops downstream spawning brown trout from the lake Rännarsjön. d) Even though grayling is the most common salmonid within the river Nätraån, we found no grayling within typical grayling habitats in the whole Nätraå-drainage above the impassable Bysjö-dam.

Natural barriers

I identified natural barriers to fish migration such as waterfalls, steep chutes over flat rocks, subsurface streamflow through bouldery areas (*SSB*)[2] and other natural types of obstacles to fish dispersal among lake outlets and streams (Fig. 8). GIS-variables were developed to indicate natural barriers (Table 1).

Fig. 8. Examples of natural barriers (*SSB* and steep chute) in streams. Here, pike is present downstream, but not in lakes (Låsjötjärnen and Kälsbodtjärnen) directly upstream these barriers.

Spawning substrate

Lake tributaries and outlets were classified as unsuitable for salmonid spawning from visual observations of stream sizes and calculations from GIS (drainage area and runoff data). Waters were considered to lack a suitable spawning substrate for brown trout and Arctic charr if the bottom material consisted entirely of sand or organic fine material.

For further details regarding physical factors see papers **I**, **II** and **III**.

GIS software

I used ESRI's ArcMap 9.2 and Arc View 3.3 with Spatial Analyst, Hydrologic modelling, Geostatistical analyst and other extensions with ODBC-connections to Microsoft Access databases to extract GIS variables in papers **II**-**IV**. Geodata is listed in Table 1.

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[2] I define *SSB* as a site where the entire stream is restricted to hyporheic flow through bouldery areas, along several meters up to several hundred meters of shoreline.

Table 1 Geodata sources used to extract central variables for predicting fish distribution. References are listed where close or fully equivalent variables relating to fish have been dealt with in previous studies. However, references have not necessarily used digital geodata to extract variables. (Cf. = compare with, as our variable differs somewhat from variable used in reference).

Variable	**Geodata**	**References** (full or close equivalent)
Adjoining open areas indicating prehistoric stocking (*AOA*)	Land-use polygons vectorized from TOPO.	Cf. similar measure of modern human shoreline disturbance but differs e.g. by including roads, lawns, fill and more (Whittier et al. 1997).
Drainage area (*DRA*)	DEM; corrected by field-observations and by using vectorized elevation contours from TOPO in combination with LAKES and STREAMS.	(Bain & Stevenson 1999).
Below Highest Postglacial Coastline? (*bHPC*)	LAKES; *HPC* Fig. 10.	Cf. marine transgressions extracted from maps (Legendre & Legendre 1984).
Maximum stream slope using fixed vertical drop (S_{V5max})	STREAMS cut using vectorized 5 *m* contours from TOPO to extract non-equal length segments.	Novel variable.
Elevation above source population (*WC-elev*)	LAKES; DEM.	Cf. similar isolation-factor of seepage lakes (Tonn et al. 1990).

Geodata acronym	**Geodata source**
STREAMS	Running waters digitized from TOPO and BLUE into line-vector shapefiles, corrected in minor extent by field-observations and AERIAL.
LAKES	Lakes digitized from TOPO and BLUE into polygon-vector shapefiles, corrected in minor extent by field observations and AERIAL.
TOPO	Topographic Maps of Sweden in scale 1:50 000 based on aerial photos. (The Swedish National Land Survey (SNLS) 1961-1967 and 2001-2004). Elevation contours were produced from aerial photogrammetry, where elevation was registered every 30 *m*, in a few areas using 60 *m* interval.
DEM	Digital elevation model was based on a 50 *m* grid derived from aerial photogrammetry with 30 x 60 *m* or 60 x 60 *m* point measurements or interpolated from elevation contours of PROP (SNLS revised 1994).
PROP	Property map of Sweden in scales 1:10 000 and 1:20 000 based on aerial photos (SNLS, 2000-2003). Elevation contours were produced from aerial photogrammetry as TOPO.
AERIAL	Aerial photos at 4,600 *m* and 9,200 *m* (SNLS, 1999-2003).
BLUE	Roadmap in scale 1:100 000 based on aerial photos (SNLS, 2000-2004).

Statistical approaches

I used Chi-square, Pearson and Fisher's exact for robust testing of general hypothesis in papers **I** & **II**. Next, I used classification trees for non-linear multivariate modelling of physical, chemical and biological factors in paper **II**, and for extracting the optimal GIS-extracted physical (connectivity-related) factors in paper **III**. Furthermore, I employed partial least squares regression (PLS) in papers **II** & **III** as a complementary multivariate modelling approach. I also utilized Discriminant Function Analysis in paper **III** as a complementary multivariate modelling approach to verify the extremely good fit of connectivity and pre-historic stocking variables generated by classification trees. I used ANOVA in paper **III** to rule out any correlation between nutrient level and *AOA*. With Moran's *I*, I assured that the multivariate analysis and hypothesis testing in paper **II** was not compromised by spatial autocorrelation. I also performed an analysis of spatial autocorrelation with Moran's *I* and clustering with Getis-Ord General G in paper **III**. I modeled extinction-risk from altitude with logistic regression in paper **II**, and in paper **IV**, correlations between fish communities and lake morphometry variables with univariate and multiple logistic regression using model selection with Akaike's *AIC*. Finally, the area under "the True Skill Statistic" (TSS) was employed in order to assess extinctions of salmonids and predictive performance of hierarchical filters.

Results - Summary of papers

I.

In this paper, I used three methods to extract baseline data by collecting historical evidence which enabled assessments of human-induced chemical, physical and biological impacts on biodiversity, in this case on brown trout. I validated historical maps, historical documents and interviews with testfishing results and enabled large temporal and spatial scale reconstruction of the baseline distribution of lacustrine brown trout populations among 1 509 lakes. My large number of sources and methods comprehensively validated the historical evidence collected for the period 1672-2000. For example, in cases where *Rö* or other dialectal terms commonly used for brown trout were part of lake names, at least a 92 per cent had historical or present brown trout populations, compared with 11 per cent when lakes were randomly chosen. Data suggest that the distribution of brown trout lakes under pre-industrial natural conditions was stable until the 1930s when extinctions became evident. I estimated the extinction rate among native brown trout to exceed 3 % lost populations per decade between 1920-2000. Limnological surveys indicated that the human impact from non-native species was most important for extinctions, more devastating than all recorded chemical and physical human impact combined. Validated historical evidence, such as historical names, fishers' knowledge and documentary evidence, combined with limnological data proved powerful in revealing large scale temporal and spatial patterns.

II.

The results suggests a long-term detrimental impact of an introduced exotic species on brown trout populations. It provides evidence for that brook charr (named ‘brook trout’ in papers **II & IV**) was associated with extinctions and displacement of brown trout. Extinctions were 10 times more frequent (20% vs. 2%) in lakes that were exposed to brook charr. I estimated the time-lag (mean: two decades) between first record of brook charr introduction and subsequent extinction of brown trout in each lake. From estimated extinction rates applied to specific cohorts of lakes (cohorts divided into time intervals since brook charr introduction), I predicted that between four and five more brown trout populations would be lost in the area by the year 2050. Results indicate that brown trout populations at higher altitude were more sensitive to impact from brook charr. Multivariate analysis tools like classification trees and PLS allowed me to screen for effects of a large number of additional variables. However, I could not detect any effects of other environmental factors e.g. drainage area, water chemistry, stocking of rainbow trout, fish species community assembly, migration barriers, fishing intensity or lake morphometry on brown trout extinction.

III.

In this study, the incidence of pike in a lake was determined as a function of the lake's connectivity and not its in-lake habitat. I demonstrated that the ability of pike to colonize upstream locations and its presence–absence in lakes could be accurately modelled based on landscape features derived from maps. I constructed a model that predicted the incidence of pike in lakes with stream-connections with 95% accuracy, based mainly on a single variable (S_{V5max}) that measures the minimum distance found between 5 m elevation intervals along watercourses from nearest downstream source of potential immigrants. In lakes without stream-connections, a variable (*WC-elev*) that measures the elevation from nearest downstream source of potential immigrants, was the best predictor. I validated models with retrospective whole-lake experiments involving introductions and extirpations (by rotenone) of pike, as well as with the natural distribution of pike in 1365 lakes within 26 drainage basin networks. Successful model validations in these drainage networks were attained via highly predictable potential sources of pike (i.e. lakes below the highest postglacial coastline with areas >0.5 and >1 km^2). I discovered a previously undescribed type of dispersal barrier - "subsurface streamflow through bouldery areas" (*SSB*) which provides a possible explanation for how reaches with low slopes can inhibit upstream invasion even in the long term. Most lakes lacking pike, but misclassified as having pike based on low S_{V5max}, were isolated from downstream sources of pike by *SSBs*. I also constructed and validated a GIS-variable - "the prehistoric stocking indicator" (*AOA*), for predicting unregistered stocking activity. At least 11% of all pike populations above the highest post-glacial coastline were indicated by *AOA* to have resulted from unregistered introductions. These results also revealed that at least 50% of all lakes in this boreal landscape were historically isolated by dispersal barriers to pike and other species with equal or less dispersal capacity.

IV.

In this study, I detected a large-scale pattern of non-coexistence with salmonid communities and the keystone predator northern pike among 1 029 lakes. I repeatedly verified the mutually-exclusive species distribution patterns from results of whole-lake interventions with rotenone and introductions. Essentially, pike rarely coexisted with salmonids and prevented self-sustaining populations of brown trout, brook charr, Arctic charr and grayling in lakes. High connectivity to pike (derived from maps, see paper **III**) largely predicted the absence of lacustrine salmonids and resulted in non-salmonid lake fish communities. I could predict fish communities with high accuracy using two out of three hierarchical filters which a species must pass to be present. The two filters, connectivity and species-coexistence, were superior predictors while in-lake habitat (chemicophysical factors) did not predict as well. My detailed, large-scale data of water-quality (lakes ranging from highly acid-neutral, clear-murky and ultraoligotrophy-eutrophy) did not relate well to either salmonid or non-salmonid waters. The one exception being the subset of lakes (2%) where salmonids had gone extinct and where pH (median 5.0) was lower than in lakes where at least one salmonid species persisted (pH median 5.8). Predictions of fish-communities were best explained with graphic charts of connectivity within drainage networks of lakes (Fig. 9).

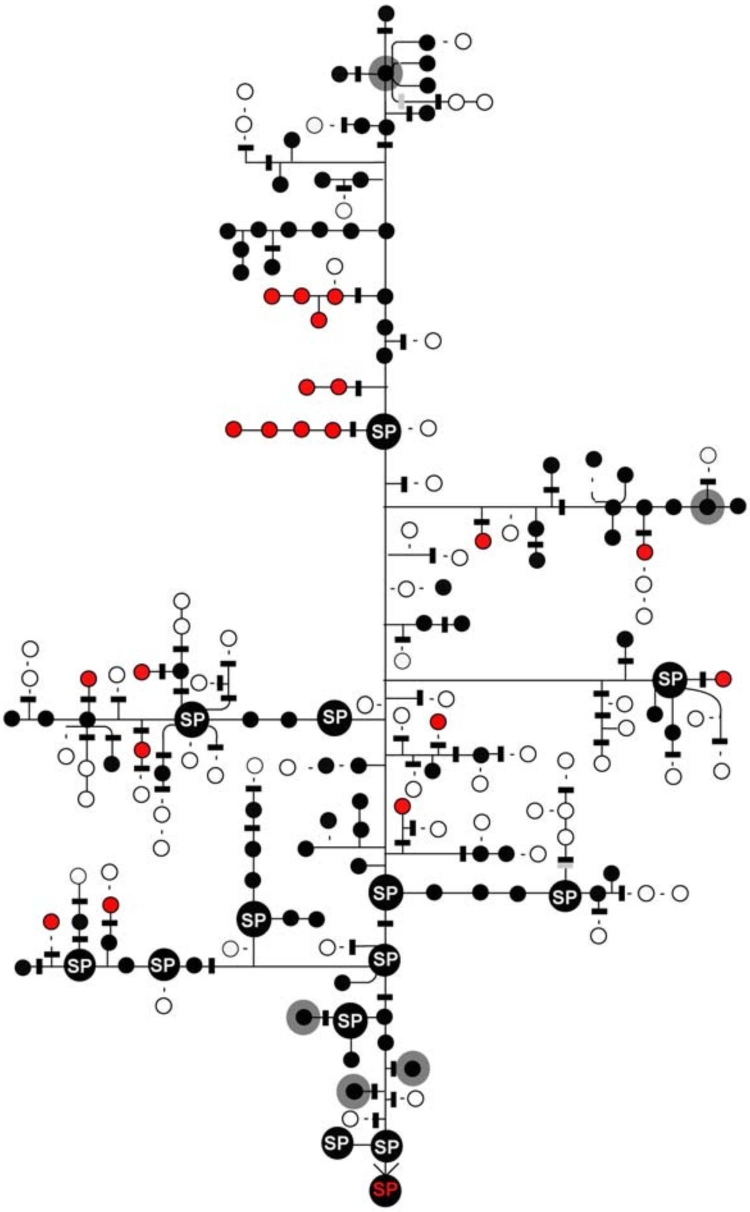

Fig. 9. Example of graphic chart of connectivity among the lakes in Nätraån. Modified from Fig. 5 in paper **III**, by indicating brown trout with red circles and non-pike lake outlets where theoretical mean annual flow < 9 L s^{-1} is represented with discontinuous lines. Large circles (SP) represents lakes and the sea (bottom circle) that are potential source-populations of pike (predicted post-glacial refuges) and starting points in the linear analysis of connectivity. Black circles are lakes with pike. Residual lakes, i.e. unfilled small circles, are lakes without brown trout or pike. Black-filled bars represent barrier indicators ($S_{V5max} \geq$ 6.6%). Grey bars represent barriers (*SSBs*) not predictable with GIS. Arrow points in the streamflow direction.

Discussion

At the watershed level, non-fragmented landscape-scale and historical fish species occurrence data are often incomplete or unavailable. Even in such vastly studied watersheds such as those around the Great lakes basin, multiyear existing datasets are rare or non-existent (Smith & Jones 2007). This suggests a general lack of such large-scale spatial and temporal data worldwide (searches: e.g. FishBase 2008-05; ISI 2008-05). Due to the general lack of field-data, Kottelat (1994) and others caution against “desktop biologists” (use of ungrounded data or unreliable “Red Lists”) while they stress proactive field survey work to provide more facts and fewer approximations concerning freshwater fishes. Missions to determine the entire fish community distribution in complete landscapes with thousands of lakes, may be prohibitively resource and time-consuming (e.g. several decades of man-years following standardized procedure according to Appelberg 2000). Revealing historical distributions, logically constitutes even more demanding tasks. Reconstructing the historical and current distribution of fish communities is nevertheless crucial, because information about what has actually been lost and why, is necessary for management and rebuilding natural ecosystems as well as for monitoring future changes (Pitcher 2001). Without proper assessments of baseline distributions, it is difficult to see how local extinctions can be determined.

Is it feasible to determine and validate a historical baseline?

In this thesis I demonstrate that the pre-industrial baseline of lacustrine fish distribution can be estimated and validated from historical and current sources using multiple methods at large spatial scales involving thousands of lakes: for brown trout (**I,II**), for a keystone piscivore (**III**), for fish communities (**IV**). For example, estimates of historical baselines may be collected from maps, historical documents, interviews and questionnaires (**I**-**IV**). More time-consuming face-to-face interviews (common in **I**-**IV**) involving collaborative fieldwork and workshops to extract local ecological knowledge can provide high-quality long-term temporal windows to evaluate fish population persistence (Fraser et al. 2006). Several years of interviews with knowledgeable fishermen underpinned by several decades of ground-truthing field surveys was used to produce highly validated baselines in this thesis. Here, these baselines were necessary for the discovery of

- hundreds of years retrospect from fish-linked lake names **(I**),
- estimates of past and future exotic-induced extinction rates **(II**),
- the connectivity variable (S_{Vimax}, **III**),
- indications of pre-historic major human impact - the *AOA*-variable (**III**),
- a previously undescribed type of crucial fish dispersal barrier (*SSB*, **III**),
- revealing the relatively minor impact from chemical in-lake factors in comparison with connectivity and biotic factors and (**II**, **III**, **IV**),
- the finding of rotenone promoting the establishment of salmonids (**IV**),
- the absolutely overruling impact exerted by a keystone piscivore (**IV**).

Many other studies also show that pursuits of historical baselines may be very rewarding (e.g. Pitcher 2001; Hesthagen & Sandlund 2004).

Windows to the past - how far back in time do we see?

With first-hand interviews I show that it is possible to extend a historical perspective eighty years or so back in time, if properly validated. Historical documents, specifically taxation records (Fig. 4), reach back five centuries. The oldest useful maps I found were dated more than three centuries ago (examples in Fig. 3). Oral tradition and customary processes how place-names are set onto maps suggests that these names are older than the maps they were written on. It has been assumed that faunal place-naming is a relatively immediate exercise that coincides with human colonization (Cox et al. 2002). Evidence indicate that the historical baseline I report for brown trout may even extend several thousand years back in time. Independent data supports this hypothesis: evidence from ^{14}C-dating of settlements, isostatic uplift and other data deciphered together with the prehistoric, 1 900 years old, fishers' name-complex found in the heart of the study area (Edlund 1997), and essentially the historic implications of the connectivity model (**III**) and its consequences (**IV**)).

This baseline will possibly extend further back in time if present connectivity has been temporally stable and does not differ much from the specific connectivity that fish experienced thousands of years ago. The strong signal of present connectivity may reflect that the geomorphology and hydrology, with the exception of land upheaval, have been stable during the postglacial period in this study area. With most of the study area situated on stable primary archean rock, the rate of stream capture is assumed to be insignificant. Also the rate of lake-tilting has been low (Bergman et al. 2003). Ice-dammed lakes that may have provided dispersal routes, were few and small in this area (Lundqvist 1987). Furthermore, there is no evidence within the study area for sluicing up to lakes above the highest post-glacial coastline (*HPC*, Fig. 10). The geographical accuracy and timing of *HPC* is supported by independent very diverse data-sets that define glacial relict distribution range ends of *Mysis relicta*, *Pallasea quadrospinosa, Limnocalanus macrurus, Gammaracanthus lacustris*, smelt and vendace (**III**; trawling-data from 185 lakes between 1984-2006; unpublished LIMNOR database 2008) in relation to the location specific (longitude & latitude) extent of isostatic post-glacial uplift (239 – 286 *m*) within the study area (**III**). Glacial relicts, because of their restrained (largely nonexistent) upstream dispersal are with few exceptions only found below *HPC* (Ekman 1922).Thus, *HPC* is a fundamental effective predictor for historical species distributions which I use to explain fish communities (from sources of pike) in this thesis. Finally, in strong support of a stable post-glacial connectivity, is that the observed deviations (mainly key piscivore omission errors) from pure connectivity-based predictions starting off from *HPC*, may be largely explained by stocking data and GIS-analysis using a measure of historical human presence (**III**). That is, lakes close to areas with consistent human presence are systematically stocked with predators (**III**; Whittier et al. 1997). In other cases (excluding rotenoned and stocked lakes), species communities are largely predicted by present connectivity from estimated *HPC* sources of a key piscivore (**III** & **IV**), which may reflect pike colonization events up to 10 000 years back in time. In my study area, the Ancylus lake covered all land below *HPC* 10 000 years ago (Berglund 2004).

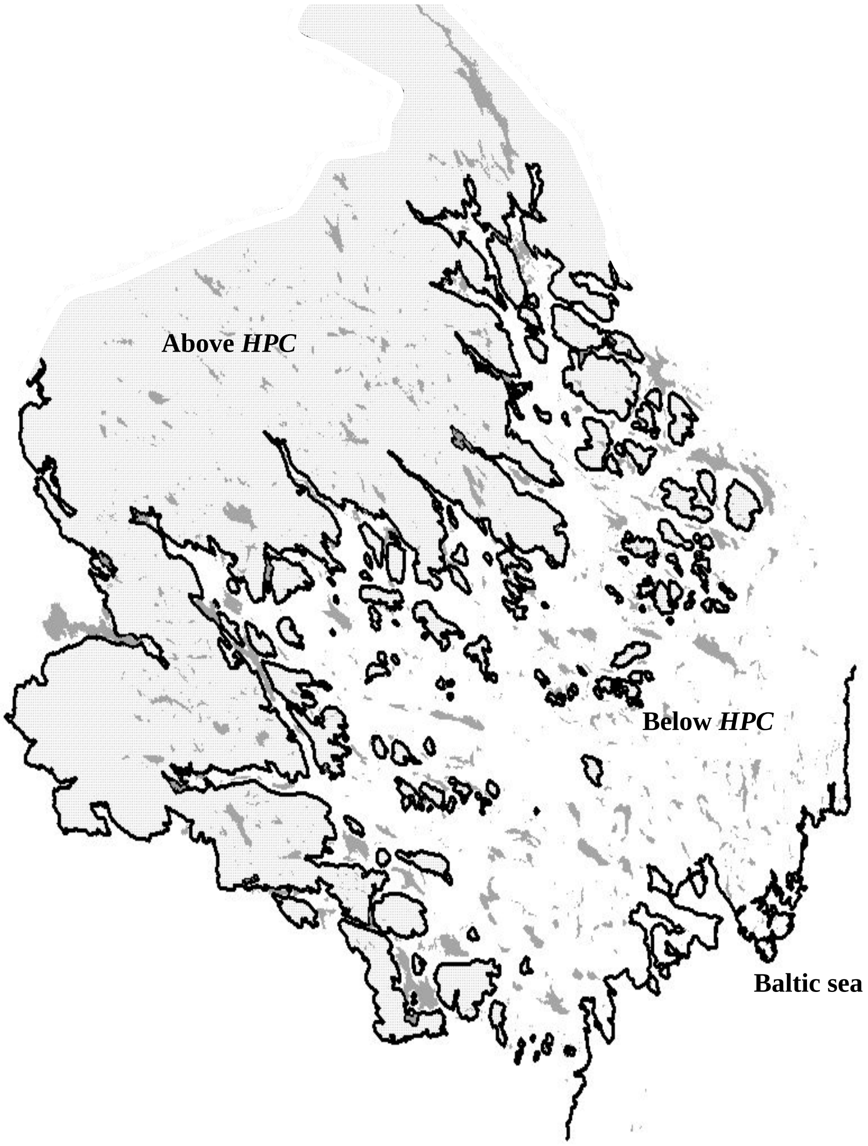

Fig. 10. Highest post-glacial coastline (*HPC*) 9 600 B.P. *HPC* is the sea shoreline existing at the time when the land mass was pressed down to its lowest level in the late quaternary stage, under the weight of the last ice age glacier. I used Arc View Spatial Analyst to interpolate (Inverse Distance Weighted) point measurements made by the Swedish Geological Service (SGU, 1978-1998). I generated isolines of different isostatic uplifts (240-281m), which I then used in conjunction with a digital elevation model to produce the coastline. I corrected *HPC* to some extent with digitized contours from Topographic Maps of Sweden in scale 1:50 000. The maximum recorded isostatic uplift in the world (286 *m*) has been recorded at the southern tip of the study area.

Fundamental importance of natural physical factors

Connectivity (1st filter)

Connectivity and isolation are opposites that can be used to describe species dispersal potential between locations. The recognition of three general types of natural lake isolation, is central to my thesis. For each of these three types, specific variables are required in order to successfully determine the degree of isolation, i.e. *HPC*, *WC-elev* and S_{Vimax}.

1) HPC:

The general absence of glacial relicts in lakes that I classify as situated above *HPC* confirms my spatial estimates of the *HPC*, which I derived starting from area-specific isostatic uplifts (SGU 1978-1998). So species presence above *HPC* is best explained by other mechanisms, e.g. S_{Vimax} and stocking activities (Fig. 11). Furthermore, even though waterbird-mediated dispersal is suggested to be essential for aquatic (non-glacial relicts, my remark) invertebrates and plants (e.g. Figuerola & Green 2002), to my knowledge, this has not been exemplified by analogous supporting data for fish dispersal. On the other hand, it has long been recognized that *HPC* explains several large scale fish species patterns among lakes (Nordqvist 1903; Legendre and Legendre 1984). In my data, many lakes below *HPC* have retained glacial relict species from the time lakes were disconnected from the sea, up to 9 600 years ago. Consequently, accurate delineations of *HPC* are essential for revealing postglacial fish species distribution patterns among lakes, particularly when generating starting points for predicting species distribution in whole drainage networks.

2) $\text{Lakes}_{\text{OUTLET(-)}}$ without connecting streams (e.g. seepage lakes):

Differences in elevation as a major factor affecting connectivity and fish species composition among lakes lacking outlet streams is recognized in other studies (e.g. Tonn et al 1990; *WC-elev*). For lakes separated from source pools with landbarriers, *WC-elev* may indicate probability that barriers are flooded. This is reflected among rotenoned lakes in paper (**III**) where low *WC-elev* (< 3,5 *m*) results in correct pike presence predictions for isolated oxbows, which are likely restocked with pike from annually reoccurring flooding-events. Furthermore, as floodplain amplitude and frequency is highly variable, the accuracy of predictions based on constant *WC-elev* will be much spatio-temporally restricted. Thus, incorporating historical floodplains in models increases predictability in certain geographical areas, at the cost of a more complicated model. However, $Lakes_{OUTLET(-)}$ predict pike presence correctly in 90% of seepage lakes without considering *WC-elev* (paper III), which may reflect that the annual floodplain-amplitude is less than a few meters in much of the study area.

3) $\text{Lakes}_{\text{OUTLET(+)}}$ connected by streams that may contain barriers (drainage lakes):

Many types of natural fish barriers are widely recognized and classified by fish biologists to be fish dispersal barriers, such as waterfalls, cascades and bedrock chutes (Powers & Orsborn 1985). I propose that the severity of these barriers may be estimated by GIS using the novel variable S_{Vimax} (**III**). For example, the newly constructed GIS variable (S_{V5max}), provides a new tool for revealing the location and severity of natural dispersal barriers to the keystone piscivore pike (and logically also barriers to other species with equivalent or less dispersal capacity). In comparison, connectedness measured as distances between lakes along straight lines or streams, appears irrelevant for establishment and extinctions (**III**). This will have large implications for future explorations of species diversity, e.g. there is little meaning in making collective generalizations on fish species assemblages of neighbouring lakes in a specific area unless barriers between lakes are known, i.e. lakes located only a few metres away from one another may contain completely different assemblages if separated by barriers (Fig. 6).

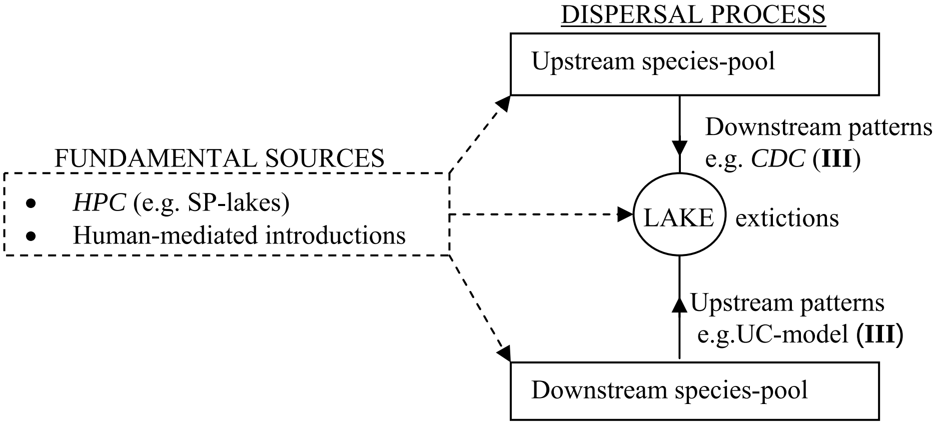

Fig. 11. Synthesis of major processes to consider when determining species connectivity to a specific lake. When judging individual lakes or streams, the connected up- and downstream source pools should be defined. From this follows that knowledge of species connectivity within the whole connected parts of the drainage network is needed to assess the potential fish community in a specific lake. Species have to be able to reach a given lake. Thus, from the time when the land upheaval set in, subsequent changes in distribution is supposedly caused by colonization factors (*HPC*, human-mediated introductions, dispersal downstream or active upstream migration) as well as local extinctions.

Temperature and altitude

Air temperatures at different altitudes may be interpolated using a general lapse rate, i.e. mean annual air temperature decrease, of 0.6 *°C* per 100 *m* elevation (Kullman & Kjällgren 2006). This is in agreement with measurements made among lakes within my study area, differing 500 *m* in elevation and Δ 3°*C* (SMHI 2006). Therefore, it may be reasonable to use altitude as an index of mean annual air temperatures among lake locations. My results infer that lower temperatures are associated with an increased extinction-risk for native brown trout exposed to exotic brook charr among lakes. Provided that brook charr had reached a given lake, no other tested biological, physical or chemical factors but altitude explains extinction-risk. This increased extinction-risk at higher altitudes confirms previously unexplained North American patterns of this species pair (Vincent and Miller 1969; Fausch 1989; Rahel and Nibbelink, 1999). Temperature has long been singled out as the central factor governing fish species distribution among lakes (Nordqvist 1903), and it has received more attention in the face of global warming (e.g. Jackson & Mandrak 2002; Chu et al. 2005). Although my results indicate that the Δ 3°C among lake locations is not enough to influence pike or salmonid vs. non-salmonid community patterns much (**III**, **IV**), at most simply salmonid species inter-coexistence (**II**). But even though the main effect of high altitude (w. brook charr) has been suggested to be related to water temperature (Vincent & Miller 1969), other untested factors related to altitude may generate differences in competitive ability or survival of fishes on a local scale and thereby fish distribution (Fausch 1989). In other studies, multiple factors show collinear relationships with altitude, particularly climate and pH (Mandrak 1995). So caution is advised when inferring causal relationships, e.g. between waterchemistry (or altitude) and fish species distribution. However, species relationships with altitude were not confounded by waterchemistry in paper **II**.

Drainage- and lake area

Besides altitude, among physical variables, only measures of connectivity improved model predictions in this thesis. Drainage size (and lakes size, my comment) is related to connectivity as lakes with larger outlet flows are less likely to be isolated seepage lakes (Tonn & Magnuson 1982). But drainage area, stream order and mean annual flow failed to add any predictive ability to models presented in papers **II** and **III**. Even though other physical variables, apart from connectivity and altitude, are of little predictive value for fish community distribution (e.g. lake area: logistic regression: $R^2 = 0.05$; **IV**), there may still exist important non-linear threshold dependent relations. I exemplify this with a threshold of lake area, >1 km^2, used as a perfect predictor for the long term survival of pike, in isolated lakes below *HPC* (**III, IV**). In these study areas, all investigated larger lakes (>1 km^2) situated below *HPC*, isolated or not, are current sources of this large keystone predator while many smaller isolated lakes have not retained pike (cf. area - extinction risk relationships: MacArthur & Wilson 1963; Tonn & Magnuson 1982). Donald (1987) suggests that lake outlet size (closely related to drainage area and stream order) may be the best indicator of salmonid colonization in lakes because it should be directly related to the quantity and quality of spawning habitat, which influence the success of salmonid colonization. The lakes lacking both pike and brown trout had the smallest drainage areas (mean annual outlet flow < 9 L s^{-1}, see unfilled circles in Fig. 9), which fits Donald's (1987) idea well.

Spawning substrate

The availability of suitably sized spawning substrate may be considered to be a limiting physical factor for establishment of self-sustainable salmonids which require clean beds of gravel, pebble or cobble for egg incubation nests (e.g. Beard & Carline 1991; Kondolf & Wolman 1993). I use the absence of proper spawning substrate in lakes and connecting streams to rule out reproduction and self-sustainability of native salmonids, which was in concordance with absences of brown trout in these waters (**I**). But the fact that brook charr may successfully reproduce on soft ooze bottoms (Fraser 1982), suggests that absence of spawning substrate cannot be used as a clearcut indicator for ruling out salmonid habitat in general.

Maximum depth

Although lake fish communities are hardly influenced by depth at all in my studies, maximum depth will certainly have a strong threshold effect on fish communities in very shallow waterbodies, as similarities to terrestrial habitats become strong. The reduced physical stability of shallow lakes as compared with deeper ones may increase local extinction risks (e.g. by dry-out or bottomfast ice). I expect that if wetlands were included in this thesis, these highly vegetated waterbodies, would needlessly confound results by signalling a threshold-dependent significance of morphometry and waterchemistry. For instance, macrophyte biomass per area and low maximum depth were the strongest predictors of O_2 decay among lakes in Meding & Jackson (2003). I avoid much of these signals by merely including lakes and employing the threshold maximum depth (≥ 2 *m*) which excludes wetlands (Blomqvist & Brunberg 1998).

Limited impact from water chemistry

My detailed and large-scale results (**II**,**III**,**IV**) refuted the widely-held ("classic") concept that water quality essentially determines fish community assemblages: that salmonids are associated with high water-quality and thus dominate the clear oligotrophic lakes, coregonids and perch succeed each other in mesotrophic conditions while they are successively replaced by cyprinids towards eutrophy (Colby et al. 1972, Ryder & Kerr 1978; Persson et al. 1991). Contrary to this previous paradigm of waterchemistry as the main determinant of fish communities, my thesis reveals overwhelming evidence for connectivity and biological factors as the main predictors for lake fish fauna assemblages. The one exception being a subset of lakes (2%) where salmonids had gone extinct and where pH (median 5.0) was lower than in the rest of lakes where salmonids still persisted (median 5.8). Apart from this minor subset of salmonid lakes, I could not detect any effects of water chemistry on the survival and distribution of either salmonids or pike, which appear widely tolerant to large ranges of acidity, nutrients and humic content of waters (**II**, **III**, **IV**). In comparison, the totally overruling chemical impact on fish community establishment and survival has been caused by rotenone (for more details, see "human impact" pg. 34). Previous explanations of lacustrine fish species presence-absence in this northern boreal region have focused on water chemistry (e.g. Tammi et al. 2003; Holmgren & Buffam 2005), while the importance of connectivity and keystone piscivores is ignored in these large scale studies. However, a lesser importance of waterchemistry is supported by other studies (e.g. Mandrak 1995), who rejects lake chemistry as an influence of species richness among ten-thousand lakes in Ontario. Note however that, in order to focus on salmonid coexistence with pike, I only included those lakes with pike or/and self-sustaining salmonids in paper **IV** (see Fig. 1 in **IV**). So the 2nd filter (**IV**) may still prove essential for modelling many small isolated lakes, ponds and wetlands (those excluded in paper **IV**). Here, the reduced chemical stability of smaller waterbodies as compared with large ones could possibly manifest increased local extinction risks (e.g. temperature and oxygen stress: Jackson et al 2001; acid stress: Eadie et al. 1986; Baker et al. 1993).

Main impact from keystone & exotic species: coexistence rules

Contrary to the previous paradigm of waterchemistry driven fish assemblages, papers **II** and **IV** reveal overwhelming evidence for coexistence-rules as the main predictors for lake fish fauna assemblages. These coexistence-rules are fundamentally structured by the keystone piscivore pike (**IV**). My analysis suggests that pike promotes the development of a non-salmonid dominated community. I reveal a piscivore-driven non-coexistence rule, which (with some exceptions, see below), predicts elimination of salmonids in lakes with pike. These results also suggest that pike may also relax severely negative perch-roach interaction, allowing coexistence of this species pair (**IV**). The evidence presented in paper **IV** strongly suggests that if pike were not present in many boreal lakes where they now dwell, then salmonid fish assemblages would prevail, deviating from the present pike-driven homogenized state with mainly non-salmonid fish communities. Prior to paper **IV**, predictions of effects of pike on lake ecosystem composition and function were largely lacking worldwide (Nilsson et al. 2008). In the previous literature, albeit not at larger-scales, odd examples (n = 1) support the importance of pike for severely altering the lake fish community and eliminating (Patankar et al. 2006; Byström et al. 2007) or promoting other fish species (n = 4, Persson et al. 2007). Furthermore, Jackson et al. (2001) find that large-scale studies support the importance of abiotic controls for shaping fish community compositions by piscivory. In agreement with this idea, I hypothesize that the importance of pike may be modified by abiotic controls such as temperature, pelagial size and geographical extent of productive refuge streams for salmonids. Although more research is required in order to assess the importance of these controls in other waters.

Even when leaving out the effect of keystone piscivores (**II**), evidence suggests that coexistence rules may be the chief determinant for species composition within salmonid communities. Here, this is supported by the 10-fold increase of extinctions of native brown trout in lakes exposed to exotic brook charr. Even though further stocking of brook charr has been stopped, my analysis suggests that existing sympatric populations may continue to pose the largest extinction threat to native brown trout. To my knowledge, this is the first scientific study (**II**) to provide more than just anecdotal evidence for brook charr being associated with extinctions and displacement of brown trout. Furthermore, in agreement with my analysis presented above concerning abiotic controls of keystone piscivores, abiotic controls also dictate the strength of impact from exotics (see “altitude” pg. 29). My analysis above concerning the overruling importance of species interaction, corresponds well to international results ranking threats to biodiversity - that the spreading of nonnative species is the most severe human impact to lakes worldwide (Sala et al. 2000). The strength of my analysis, in comparison with other studies of coexistence, is the extended temporal perspectives and inclusion of both landscape-scale patterns in whole drainage networks as well as retrospective interventions (introductions and removals) with control (unexposed to intervention) lakes. More field studies on the ecological effects of invasive fishes are urgently needed, while e.g. FishBase databases are of little use with this regard, since they reflect subjective human interests rather than objectively measured ecological effects (Garcia-Berthou 2007).

Feasibility of landscape-scale GIS-models

Single species model

First I validate archaic names on maps that identify at least a third of all brown trout populations among 1 509 lakes (**I**), which provides an important pre-industrial baseline distribution. To pick out the same amount of brown trout lakes by random sampling with multimesh-sized gillnets (Appelberg, 2000), would take approximately a decade of fulltime fishing but this effort would still miss all extinct populations and lack the temporal perspective that lake names provide. Secondly I demonstrate that it may be highly feasible to construct a landscape-scale GIS-model based simply on remotely collected DEM's and stocking data, to assess exotic-induced extinction risk to native lacustrine brown trout. Here, extinction-risk is largely a function of altitude which is associated to mean annual air temperature, while less accessible physical (e.g. lake depths) and biological (e.g. other fish species) data is largely redundant (**II**). Thirdly I demonstrate that the distribution of a single keystone species among lakes could be accurately modelled (with 95% accuracy) from map-derived variables that measure connectivity (**III**). I attained successful model validations both at the landscape-scale for many different drainage networks as well as by using retrospective interventions. Pike is a generalist with high dispersal capacity and a wide tolerance to both abiotic and biotic factors (**IV**). For example, pike do not require other prey fish species to survive (pike may shift to evertebrates and cannibalism; Casselman, 1996), nor have I found any evidence of pike being excluded by competition or predatory exclusion by other piscivore fish species in connected lakes (**III**, **IV**). Its high tolerance to a wide range of habitat in the short term (several decades), is supported by the fact that pike is easily established in isolated lakes when introduced (**III**, **IV**). Therefore, pike is an ideal fish species to use for modelling contemporary connectivity, as it should colonize those lakes it can reach at present, within wide habitat tolerance limits.

While in isolated lakes that were previously connected or stocked, extinction factor(s) (e.g. rotenone treatments), determine if pike have gone extinct. For predictions of long term (several thousands of years) survival in isolated lakes below *HPC*, decisive extinction factor(s) are associated with lake area (see pg. 30). Given the above, an advantage of choosing pike as a model organism is that mainly physical variables based on remotely collected data on fixed landscape features (e.g. DEM's) are needed, while less accessible chemical (e.g. acidity) and biological (e.g. fish species) data is largely redundant. Although I discovered a previously undescribed type of dispersal barrier (i.e. *SSB*), which I did not manage to predict using data from maps (**III**). So this type of barrier indicates that it may be problematic to construct an absolutely perfect GIS-based connectivity model unless high resolution visual data of streams is collected as well. The highly successful single species (pike) connectivity model (**III),** is a fundamental key to remote predictions of fish communities using a filtering approach (**IV)**.

Fish community model

Advancing further towards a more structured holistic framework to predict fish communities, I assess a series of three hierarchical filters (i.e. connectivity, chemicophysical factors and coexistence-rules) which fish species must pass to be present in a given lake. Here, I demonstrate that salmonid and non-salmonid fish communities can be distinguished with high accuracy using only two (connectivity and coexistence-rules) out of three hierarchical filters from map-derived data, with focus on the keystone piscivore pike (**IV**). For the first time, to my knowledge, an explanation to why these northern boreal lakes hold the specific fish communities they do, is supported by highly accurate model predictions from GIS-data at the landscape scale in whole drainage networks (**IV**). I propose that highly predictable pike-specific connectivity is the fundamental determinant that either generates salmonid (low connectivity) or non-salmonid (high connectivity) assemblages and thus dictates fish species community compositions among these lakes. Series of hierarchical filters have previously been used to predict fish communities efficiently (Tonn et al. 1990; Quist et al. 2005), and the idea to focus filters on strong interactors (i.e. "keystone species") was suggested by Poff (1997). Biotic filters are more easily invoked after the tolerances of species to abiotic factors have been established (Tonn et al. 1990). My collective results (**II**, **III**, **IV**) confirm that it may be feasible to construct predictive community models using a holistic approach with hierarchical filters that include keystone species, chemical and physical (including connectivity) determinants of species establishment and extinctions. My thesis demonstrates that community GIS-models may prove particularly feasible in situations where keystone species distribution is highly predictable from map-derived variables.

Assessment of Human Impact

Our capacity to effectively distinguish between natural and human-induced establishment and extinctions of fish species is a critical issue for prioritizing research, management and conservation of freshwaters. In this thesis, I show ways to estimate the reference states of fish species' incidence in lakes and I attain estimates of pre-industrial as well as 20th century extinction rates (**I**,**II**,**III**,**IV**). Given the landscape-scale GIS-models presented in my thesis, human impact may be more easily invoked. I invoke large scale human influences on fish species' distributions by comparing sites with and without specific human impact, specifically stocking of nonnatives, rotenone treatment, constructed barriers, large fishing pressure and low water quality. For the first time in this northern boreal region, I provide landscape-scale evidence of specific human influences that cause major extinctions of lacustrine salmonids (**IV**). It is now clear that the totally overruling extinction factor for lacustrine salmonids and thus the chief management concern here, is the spreading of nonnatives (**I**,**II**,**IV**). I conclude that spreading of exotic brook charr and the keystone species pike has extirpated many native salmonid populations, while I fail to detect any effect from the widely stocked exotic rainbow trout (**II**). On the other hand, I show that rotenone treatments result in several new establishments of salmonid communities in cases where the keystone piscivore is permanently eliminated. Construction of barriers to fish migration are also associated with a few extinctions of brown trout, while I fail to detect any effect from increased fishing pressure.

Even though extinctions of salmonids in a small subset ($n = 5$) of lakes were associated with low pH-values (**IV**), it is still unclear whether these extinctions were natural or caused by inputs of human-derived acids. In addition, a few extinctions were reversed (although the specific original stocks have been irreversibly lost) by liming, strengthening a causal link with acidity. Salmonids appear many times more sensitive to human influences than pike, for which no extinctions were detected other than by intentional removals with rotenone (**III**).

The European Water Framework Directive (WFD) requires that member states produce river basin management plans that cover the 'identification of reference conditions' for lakes: "The methods shall use historical, palaeological and other available data..." (EU 2000). I suggest that approaches presented in my thesis may contribute to WFD basin management, providing means for prioritizing in risk assessments and control programmes to combat nonnative invasions, as well as contribute to determining a reference state of species incidence and human impact in specific lakes. Hopefully, these findings may contribute to government funding and lake management actions being directed towards the main extinction risks and restoring lost populations effectively.

Future research needs

In the future, more precise topographical measurements may be used to improve model variables (e.g. S_{Vimax}) presented in this thesis, as digital elevation models (DEM's) based on airborne light detection and ranging (LiDAR) measurements in decimetres become more available (Toyra et al. 2003).

The upstream dispersal capacity of fish is mostly determined by their ability to pass high water velocities (Castro-Santos 2006) and their vertical leaping capacity (Kondratieff & Myrick 2005). Therefore, S_{Vimax}, where the fixed vertical interval V_i can be set anywhere from less than a metre up to many metres may be a useful variable in future research of natural connectivity for many different species. In the future, the new variable S_{Vimax} may be used in an objective manner to classify large-scale drainage networks as more or less resistant to invasion by natives, non-natives or specific genetic strains, where after hypotheses concerning existing species (or genetic) patterns may be tested. Radio telemetry of migrating individual fishes at different S_{Vimax} may be a faster approach to construct and evaluate S_{Vimax}, in comparison with the wait for invasions to progress and establish. In the latter case, it's possible that established populations may be confirmed first after several years or decades (**III**) or delayed until after 100 or 1000-year flows occur in lakes with low *WC-elev*, whereas the dispersal capacity of individual fishes may be tested momentarily by radio telemetry. In order to model dispersal capacity within more controlled experimental designs, it may be feasible that such radio telemetry studies be combined with construction of bypass channels with varying S_{Vimax}.

Artificial barriers that mimic natural *SSB*s need to be constructed and tested (preferably within experimental designs at varying S_{Vimax}) in drainage networks threatened by ongoing invasions of pike, in order to assess the effectiveness of *SSB*s in preventing invasion of pike.

Landscape-scale biohistorical research using place names linked to terrestrial species distribution is progressing successfully worldwide, contributing to historical and current range maps of plants, mammals and reptiles (Aybes & Yalden 1995; Gruezo 1999; Cox et al. 2002). Considering that paper **I** was the first in primary literature to employ lake names in revealing pre-industrial fish distribution, there may be much historical baseline data left to reveal (and validate) by researching fish species-linked place names worldwide.

I suggest additional studies to determine to what degree a finer 2nd hierarchical filter (i.e. less favourable abiotic in-lake habitat for pike: e.g. relatively larger pelagials and/or colder lakes) may relax the binary pike and salmonid non-coexistence rule. In future research on climate warming (or cooling) effects on salmonids such studies may be essential. Furthermore, the importance of weak acidic water for impairing detection of chemical alarm cues by salmonids (Olivier et al. 2006), potentially involving dietary odours of predatory pike and also coexistence, needs to be tested among lakes. I also suggest additional studies to reveal factors that promote high recruitment of large salmonids from pike-free areas (i.e. refuge areas where salmonids can grow to exceed the gape-size limits of pike). Such factors might modify the non-coexistence rule from binary to continuous.

I suggest that experiments to remove exotic brook charr be carried out in lakes and streams in order to assess potential re-establishment of native brown trout. The genus *Salvelinus* appears better adapted to colder climates than *Salmo* and *Oncorhynchus* (Power 1990). But there is still an information gap concerning the specific habitat factors related to higher altitudes and harsh conditions of small streams, that appear to give brook charr an adaptive advantage over brown trout. More research is needed that involves specific habitat factors (associated with altitude in my study areas), in order to determine causality and predict past, present and future establishments and extinctions of this species pair at large geographical scales.

In order to reveal additional keystone piscivores, I suggest that large-scale spatial and temporal distribution patterns of fish distributions are explored worldwide. I also suggest that such explorations are supplemented with carefully designed experiments that induce or reverse keystone effects on other species (e.g. piscivore effects on perch-roach coexistence and establishment of sticklebacks), by eliminating or adding keystone piscivores in very cautiously selected lakes and streams. Ongoing pike invasions in Alaska (Dalton 2002), Spain, Ireland and other locations may provide exceptional opportunities to study keystone-induced effects. These ongoing invasions may also provide exceptional opportunities to assess effectiveness of artificial barriers and keystone extirpation procedures.

Several opportunities may remain for using GIS to construct predictive distribution-models with fish connectivity that fundamentally determines production at other trophic levels, as fish may extirpate amphibians (Bradford et al 1998; Knapp & Matthews 2000;) and snakes (Matthews et al. 2002), depress largebodied zooplankton (Jeppesen et al. 2001) and benthic macroinvertibrate species (Bradford et al 1998; Schindler et al. 2001) as well as alter waterfowl production (Eriksson 1979).

Future studies of fish distributions should consider involving baselines. Unless integrating baselines into investigations of present species distributions, I argue that (considering increasing human impact and large natural temporal changes) much of what we will see is vague and fragmented snapshots, rather than approaching a more complete picture.

Swedish summary – Svensk sammanfattning

Spens, J. 2008. Att nyttja GIS-verktyg för att prediktera etablering och utrotning av sjölevande laxfisksamhällen: påverkan från nyckelarter, exoter, kemiska & fysiska faktorer. Doktorsavhandling. ISSN: 1652-6880 ISBN: 978-91-86195-04-5. Originaltitel: Using GIS to Predict Landscape-scale Establishment and Extinctions of Lacustrine Salmonids: Impact from Keystone Species, Exotics, Chemical & Physical Factors.

En ökad förståelse för laxfiskars stränga livsmiljökrav behövs för att skydda och sköta många sötvattens-miljöer. I min avhandling har jag använt tidsmässigt och geografiskt storskaliga data för att utvärdera vilka nyckelfaktorer som avgör förekomsten av självreproducerande sjölevande laxfiskar. 7 650 km^2 avrinningsområden undersöktes vilka inkluderar mer än tusen sjöar i norra Ångermanland. Jag använde multivariata analysverktyg som Classification Trees, Partial Least Squares regression och multivariat logistisk regression att modellera effekterna av inhemska och införda arter samt kemiska och fysiska faktorer som kan styra fiskarters etablering och utdöenden. Historiska källor, dvs. historiska arkiv med dokument och kartor samt intervjuer med lokala fiskare i kombination med senare års limnologiska undersökningar möjliggjorde beräkningar och valideringar av nuvarande och förindustriell utbredning samt utrotningshastigheter. Öringens utrotningshastighet ökade från en obetydlig nivå i förindustriell tid, upp till mer än 3% förlorade populationer per decennium mellan 1920-2000. Med hjälp av dessa datakällor, kunde jag knyta utrotningar till olika typer av mänsklig påverkan. Långsiktig påverkan från införandet av amerikansk bäckröding (*Salvelinus fontinalis*) resulterade i en 10-faldig ökning av utrotningshastigheten bland inhemsk öring.

Jag konstruerade geografiska informationssystems (GIS)-variabler som kunde förutsäga nyckelarten gäddans utbredning. Gäddan styrde i sin tur förekomsten av laxfiskar bland sjöarna. Storskaliga utbredningsmönster och historiska mänskliga ingrepp med utsättningar, utrotningar och (åter)kolonisationer av gädda och laxfiskar, visade tydligt att gädda förhindrar självreproducerande populationer av salmonider i dessa sjöar. Med hjälp av ”hierarkiska filter” ges en ny, mycket förutsägbar förklaring till varför dessa nordliga boreala sjöar hyser de särskilda fisksamhällen de nu gör. I huvudsak är naturliga vandringshinder den viktigaste och avgörande faktorn som antingen genererar laxfisk- (låg konnektivitet) eller icke-laxfisk- (hög konnektivitet) samhällen och styr därmed fiskartsammansättningen i sjöarna. Däremot är vattenkvalitet (sjöarna varierar från starkt sura till neutrala, klara till mörkbruna och ultranäringsfattiga till näringsrika) och sjömorfometri (från ytliga små dammar till större 53 *m* djupa sjöar) inte bra indikatorer för laxfisk- eller icke-laxfiskvatten annat än i några få undantagsfall. Sammanfattningsvis rekommenderar jag därför att konnektivitet (vandringshinder-analys med t ex S_{Vimax} = maximal vattendragslutning mätt i fasta vertikala intervall), bör övervägas vid regelmässig karakterisering av sjöar, där t ex pH och vattendjup rutinmässigt används idag.

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This thesis reveals fundamental factors that determine the distribution of self-sustaining lake-living salmonids. Large-scale temporal and spatial data provided estimates and validations of pre-industrial baseline distributions and extinction rates. Nonnative species impact on the survival of brown trout (*Salmo trutta*) populations greatly exceeded any impact from natural causes or water chemistry. Novel Geographic Information System (GIS) tools were the best predictors of landscape-scale distributions of the keystone species pike (*Esox lucius*), which in turn largely governed salmonid distribution among lakes.

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