Havs
och Vatten
myndigheten

Compromising Baltic salmon genetic diversity -

conservation genetic risks associated with compensatory releases of salmon in the Baltic Sea

Havs- och vattenmyndighetens rapport 2012:18

Compromising Baltic salmon genetic diversity -

conservation genetic risks associated with compensatory releases of salmon in the Baltic Sea

---

Anna Palmé
Lovisa Wennerström
Peter Guban
Nils Ryman
Linda Laikre

Havs- och vattenmyndighetens rapport 2012:18

Havs- och vattenmyndigheten
Datum: 2012-12-20

Ansvarig utgivare: Björn Risinger
ISBN 978-91-87025-19-8

Havs- och vattenmyndigheten
Box 11930, 404 39 Göteborg
www.havochvatten.se

Preface

A majority of the original wild Baltic salmon populations has gone extinct. Historically, 84 rivers flowing into the Baltic Sea have harbored Atlantic salmon, but currently only 10 of these maintain self sustaining wild natural populations in safe numbers. Large scale releases of salmon are carried out in the Baltic mainly to compensate for natural reproduction that has been lost due to hydroelectric power plants that are blocking previous migratory routes. These compensatory releases are made in accordance with water court decisions. The aim of this study is to summarize what is currently known regarding the genetic risks associated with large scale releases of salmon in the Baltic Sea.

This report has been produced by the Division of Population Genetics, Department of Zoology, Stockholm University on request by the Swedish Agency for Marine and Water Management. The report is part of the Swedish flagship project "to ensure sustainable fishing in the Baltic Sea" within the framework of priority area nine of the EU Strategy for the Baltic Sea Region. The views expressed in this report are those of the authors and do not necessarily represent the official position of the Swedish Agency for Marine and Water Management.

Funding was provided by the Swedish Agency for Marine and Water Management and the BaltGene research program (funded by BONUS Baltic Organisations' Network for Funding Science EEIG). Additional support was obtained from The Sida Baltic Sea Unit and from the , the Nordic Council of Ministers, and Stockholm University.

I hope that this report will be useful in the future management of Baltic salmon and during the finalization of the European Union multiannual plan for the Baltic salmon, COM(2011) 470 final.

Gothenburg 2012

Ingemar Berglund,
Director, Planning Department,
Swedish Agency for Marine and Water Management

CONTENTS

1. Summary

Many aspects need to be considered when evaluating the consequences of halting compensatory releases of salmon in the Baltic area. The present report focuses strictly on genetic concerns associated with large scale salmon releases.

A majority of the original wild Baltic salmon populations, i.e. populations of Atlantic salmon (*Salmo salar*) in the Baltic Sea, has gone extinct. Historically, 84 rivers flowing into the Baltic Sea have harbored Atlantic salmon, but currently only 10 of these maintain self sustaining wild natural populations in safe numbers (CCB 2012). Large scale releases of salmon are carried out in the Baltic region to increase productivity of separate populations and to compensate for natural reproduction that has been lost due to hydroelectric power plants that are blocking previous migratory routes.

Already in the 1980s observations of pronounced genetic differentiation between populations inhabiting different rivers, coupled with indications that salmon hatchery stocks are genetically divergent from the wild populations they were meant to represent, have warranted conservation genetics researchers to warn against potential negative effects of large scale releases (Ståhl 1981, 1983, 1987). In brief, current large scale releases can cause the following four types of genetic risks for native populations: *1*) loss of genetic variation, *2*) loss of adaptations, *3*) change of population composition, and *4*) change of population structure (Laikre et al. 2010). These adverse genetic impacts have been recognized and documented for salmonid fishes for decades (Ryman 1981; Ryman & Utter 1987; Hindar et al.1991; Waples 1999; Naish et al. 2008; Nielsen & Hansen 2008). In 2011 these potential risks of large scale releases gained attention when the European Commission put forward a proposal of phasing out all compensatory releases of salmon in the Baltic area (European Commission 2011).

We have compiled and reviewed information regarding compensatory releases of salmon in Swedish rivers including spatio-temporal genetic variability patterns of wild and hatchery salmon populations in the Baltic region. We review and synthesize scientific information from both peer-review and “gray” literature, and have used available genetic data from both published and unpublished studies to address the following main questions:

- What is currently known regarding the spatio-temporal genetic variability patterns of Atlantic salmon in the Baltic Sea?
- How has the loss of salmon populations affected the overall capacity for Baltic salmon to maintain genetic variation?
- What are the effects of releases on genetic variation between and within wild salmon populations?
- How much of the overall genetic variability of Baltic salmon exists exclusively in hatcheries or is maintained only through breeding-release operations?

- Based on current genetic knowledge, what recommendations can be provided with respect to the proposal from the European Commission to halt compensatory releases of salmon in the Baltic?

A total of 37 scientific studies on Baltic salmon genetic diversity have been identified. "Gray" genetic literature on Swedish salmon populations comprises seven additional reports. Together they cover genetic information from populations representing 35 Baltic river systems (Rivers Umeälven and Vindelälven counted separately) and c. 23 000 genotyped individuals. The main conclusions from these studies are that the Baltic salmon is genetically divergent from other Atlantic salmon populations and that there is a high degree of genetic structuring between populations in different rivers within the Baltic area. Further, there is a hierarchical grouping of populations in the Baltic, and three larger genetic groups, corresponding to populations in the north, east and south Baltic Sea have been found.

In Sweden, compensatory releases of salmon are performed in eight rivers flowing into the Baltic Sea and a total of more than 1.8 million salmon smolt are released annually in Sweden. Despite the hydropower companies’ policy to use local strains, fish of non-local origin is sometimes released. Further, in some hatcheries relatively few spawners are used, which may lead to an increased loss of genetic variation. Information regarding the number of released salmon, number of females and males used in rearing, and strains used for stocking is not easily accessible, and therefore assessment of genetic effects of large scale releases is not straightforward

Our analyses of published and unpublished genetic data indicate that a large part of the original genetic variation in Baltic salmon has already been lost due to extinction of individual populations and reduction in population sizes. There is a clear pattern of isolation-by-distance among wild populations, whereas no such pattern is found among hatchery stocks. Further, hatchery stocks typically exhibit lower genetic variation and are less divergent from each other than wild populations. However, hatchery stocks can harbor unique genetic variation and may thus be important to conserve.

The genetic effects of releases have not been monitored in the Baltic, but one scientific study indicates strong genetic homogenization of wild populations. Many of the changes of Baltic salmon gene pools occurred prior to the time when molecular genetic studies were possible. Thus, we are not likely to ever clarify exactly the changes that have occurred. Studies of salmonid releases in other parts of the world have in several cases documented altered genetic composition and reduced variability and viability. The extent of this threat needs further investigation. Until such data is available large scale releases should be stopped in line with the precautionary principle, provided that essential actions are implemented to protect remaining wild stocks from e.g. overharvest. Likewise, as many previous spawning areas as possible need to be restored, to safeguard the continued existence of Baltic salmon.

1.1 Conclusions and recommendations

We have evaluated the conservation genetic risks associated with compensatory releases of Atlantic salmon in the Baltic Sea and the conclusions from this work can be summarized as:

1. The Atlantic salmon in the Baltic Sea is genetically irreplaceable in that it represents one of three major evolutionary units of the species. Each present salmon river harbors at least one genetically distinct population.
2. The extinction of a large number of wild populations has been harmful to the Baltic salmon; the capacity for retaining genetic variability has decreased as a consequence of a reduced genetically effective population size of the global population.
3. The global and the local effective population sizes have been further depleted through decreasing size of remaining local populations.
4. From a conservation genetics perspective the compiled information suggests that the proposal of the European Commission to halt compensatory releases of salmon in the Baltic is logical and sound.
5. Large scale releases constitute a potential threat to Baltic salmon genetic diversity. This is due to the genetic risks associated with *i)* gene flow from released hatchery stocks into wild populations, and *ii)* risks of overharvest of weak, wild populations because of increased numbers of salmon in the Baltic following the releases.
6. Little research has been devoted to empirically assessing the genetic effects of compensatory releases in the Baltic Sea, but observations from large scale salmonid releases in other geographical areas include: *i)* genetic homogenization of previously diverged populations, *ii)* complete or partial replacement of native gene pools, *iii)* break down of adaptations to local conditions, and *iv)* spread of diseases and parasites reducing absolute and effective sizes of native populations.
7. Comparisons of wild and hatchery stocks of the same river show that the genetic divergence between hatchery stocks is generally smaller than between wild ones. Further, there is a clear pattern of isolation-by-distance among wild populations, whereas no such pattern is found among hatchery stocks, suggesting that the natural genetic structure has not been maintained in hatcheries. This genetic homogenization might affect the capacity for local adaptation.
8. We have found only one monitoring study on genetic effects of compensatory releases in the Baltic Sea. In that study the scientists report a strong homogenizing effect on the genetic composition of the wild population in the River Vindelälven. This population became increasingly similar to hatchery stocks released in the neighboring area, and migration from hatchery stocks into the wild population was estimated as over 10 percent.
9. In most Swedish rivers the total number of released individuals, including smolt, fry, and eggs, exceeds the number of salmon obliged to be released

according to court decisions. Crude estimates of effective population sizes (based on sex ratio only) show that Swedish salmon hatchery stocks frequently do not reach scientifically accepted levels for retaining genetic variation.

10. An unknown proportion of the current gene pool appears to be maintained exclusively through hatchery operations. Removing hatchery stocks will result in loss of genetic variation, but the extent of such loss remains unclear.
11. Strategies are urgently needed for maintenance of genetic variation that only exists in hatchery stocks, and for restoring as much as possible of the global Baltic salmon population through re-establishing spawning areas and opportunities for natural reproduction.

Based on our evaluation of the genetic risks associated with large scale compensatory releases of salmon in the Baltic we provide the following recommendations:

1. Compensatory releases of salmon in the Baltic should be phased out.
2. Releases in remaining salmon rivers that support wild, viable populations should be prohibited.
3. Conservation releases to support or re-establish weak/extinct populations can be used to protect and maintain as much as possible of the remaining Baltic salmon gene pool. The need for such releases should be evaluated on a case by case basis.
4. When releases are carried out they should always be monitored with respect to genetic effects, including those from supportive breeding because of the risk of reducing the genetically effective size of local populations.
5. The conservation genetic goal for Baltic salmon should be to create a global population that is as efficient as possible with respect to retaining genetic variation on a local and global scale.
6. A change of present fishing pressure is of key importance for the success of measures taken to improve the situation for, and the genetic status of, the Baltic salmon. It is critical that fishing pressures are modified in relation to changes in smolt production if compensatory releases are halted.
7. As many previous spawning areas and local populations as possible should be re-established.
8. The fate of individual hatchery stocks must be determined on a case by case basis. This can include *i)* using hatchery material for restoring or restocking rivers that presently do not support self sustaining populations, *ii)* keeping hatchery brood stocks or sea ranched populations as gene banks during a restricted period of time, and *iii)* prioritizing hatchery stocks with respect to their contribution to the global gene pool, and if necessary focus conservation actions on those stocks that contribute significantly. These operations must be coordinated and monitored, and may imply meta analysis using existing information and/or collection of new data for

assessing the degree of current genetic similarity between wild and hatchery stocks.

9. A genetic advisory board should be initiated that includes population and conservation geneticists from all the Baltic countries. This board should supervise and coordinate national and international efforts to restore and maintain Baltic salmon gene pools as well as development of means and methods for consistent documentation and record keeping on hatchery breeding and release operations.
10. A review of existing archives of Baltic salmon tissue samples and genotypic data should be performed as soon as possible. Such resources provide an important basis for further genetic monitoring of Baltic salmon genetic biodiversity. Similarly, identifying the most critical gaps in currently available genotypic data constitutes a natural and important next step following the present synthesis report.
11. Several research issues remain to be addressed. Important cost effective work can be carried out without large scale additional genetic screenings building on already available genetic data.

1.2 Contact and further reading

Anna Palmé and Lovisa Wennerström contributed equally to this report. Lovisa Wennerström can be contacted at lovisa.wennerstrom@zoologi.su.se. Anna Palmé is currently affiliated with the Swedish Agency for Marine and Water Management and can be contacted at anna.palme@havochvatten.se. Linda Laikre and Nils Ryman can be contacted at linda.laikre@popgen.su.se and nils.ryman@popgen.su.se, respectively.

Other publications generated within the framework of the present assignment include:

Palmé A, Wennerström L, Guban P, Laikre L (editors) 2012. Stopping compensatory releases of salmon in the Baltic Sea. Good or bad for Baltic salmon gene pools? Report from the Baltic Salmon 2012 symposium and workshop, Stockholm University February 9–10, 2012. Davidsons Tryckeri, Växjö, Sweden.

Palmé A, Wennerström L, Guban P, Ryman N, Laikre L. 2012. Conclusions on conservation genetic risks associated with compensatory releases of salmon in the Baltic Sea. A brief summary of a synthesis report to the Swedish Agency for Marine and Water Management. Department of Zoology, Division of Population Genetics, Stockholm University, Sweden.

These reports can be downloaded from: www.popgen.su.se

2. Introduction

This report concerns genetic biodiversity of Atlantic salmon (*Salmo salar*) in the Baltic Sea in relation to the recent suggestion from the European Commission to halt compensatory releases of salmon in the Baltic area. Genetic information is crucial for evaluating consequences of such a ban. Several aspects need to be considered when evaluating the present proposal including ecological, socioeconomic, and commercial and sport fisheries related issues. Also, the specific suggestion of phasing out compensatory releases within a seven year period must be evaluated. However, our current assignment is of a strictly genetic nature.

We review and synthesize what is currently known regarding genetic variability of Baltic salmon and how this variability is affected by large scale releases of hatchery reared individuals. Specifically, we evaluate the genetic risks of large scale releases and provide recommendations based on this synthesis.

2.1 Background

The Atlantic salmon is one of the most well studied species world wide with respect to population genetic structure. A study of genetic variation and possible spatial intraspecific differentiation based on quantitative characters was presented in the beginning of 1970s (Ryman 1972). Soon thereafter, introduction of new techniques such as protein electrophoresis made it possible to explore allelic variation in distinct loci and these techniques were adapted to tissue analysis of salmonids (Allendorf et al. 1976). The first multi loci genetic studies of Atlantic salmon in the Baltic were carried out in the early 1980s and showed pronounced genetic differentiation between populations inhabiting different rivers (Ryman 1981, Ståhl 1981). Early genetic studies also indicated that hatchery salmon stocks were genetically differentiated from the wild populations they were meant to represent (Ståhl 1983, 1987).

These observations have warranted conservation genetics researchers to warn against possible losses of intraspecific biodiversity (=genetic diversity) following human impact on natural populations. Warnings have included possible effects of river dam constructions that prohibit natural reproduction and thus can result in loss of genetically unique populations, and large scale compensatory releases that are carried out to compensate for lost natural reproduction but which can result in negative effects on native gene pools. Such negative effects can arise if the released individuals *i*) do not represent the natural genetic composition in areas of release and thus can change the genetic composition and/genetic structure, *ii*) carry parasites that can spread to the native populations resulting in reduced effective sizes, *iii*) do represent the natural populations genetically but reduce the effective population size through supportive breeding effects, or *iv*) if the released individuals result in increased straying among natural populations and thus “unnaturally” inflated levels of gene flow (Chapter 7; Ryman & Laikre 1991; Laikre et al. 2010).

These warnings have remained neglected by authorities and politicians for several decades. However, during recent years several efforts have been made to highlight the genetic situation of the Atlantic salmon in the Baltic Sea (Swedish Board of Fisheries 2010) and in August 2011 the European Commission put forward the “Proposal for a Regulation of the European Parliament and of the Council establishing a multiannual plan for the Baltic salmon stock and the fisheries exploiting that stock” (European Commission 2011). This proposal includes the suggestion that releases of salmon in Baltic rivers should be phased out over a seven year period. Exceptions are conservation releases that are carried out to re-establish populations in rivers that have lost their natural population or to support weak natural populations. Populations subjected to such conservation releases must, according to the proposal, be monitored genetically to be able to evaluate effects of the release on remaining natural gene pools (European Commission 2011).

The European Commission also proposes to allow releases in rivers with remaining wild salmon populations. The rivers with wild salmon are listed in Annex I of the proposal. The suggestion states that “released smolts in each river shall not exceed the estimated potential smolt production capacity of the river”, and further that “stocking shall be conducted in a way that safeguards the genetic diversity of the different salmon river stocks taking into account existing fish communities in the stocked river and in neighboring rivers while maximizing the effect of stocking”.

2.2 Political background of suggestion on halting compensatory releases

Below is a brief summary of the political background to the current discussion on phasing out compensatory releases of salmon in the Baltic region and the genetic effects of maintaining or halting releases.

2.2.1. The Baltic salmon flagship project of the former Swedish Board of Fisheries (now the Swedish Agency for Marine and Water Management)

The European Union launched an EU Strategy for the Baltic Sea Region in 2009 (Council of the European Union 15265/1/09 REV 1; http://ec.europa.eu/regional_policy/cooperate/baltic/index_en.cfm) and priority area 9 of this strategy focus on reinforcing sustainability of agriculture, forestry and fisheries. Within the framework of this work the Swedish Board of Fisheries (now the Swedish Agency for Marine and Water Management) launched a flagship project on enabling sustainable fishing of salmon including regional coordination efforts to implement the EU Baltic Sea salmon management plan. A workshop was held at the HELCOM headquarters in Helsinki in October 2010 and a main conclusion from that workshop was that the genetic risks of salmon stocking needs to be recognized and addressed to enable biologically sustainable management of Baltic salmon (Swedish Board of Fisheries 2010).

2.2.2 The European Commission proposal on Baltic salmon stocks

The European Commission put forward the document “Proposal for a Regulation of the European Parliament and of the Council establishing a multiannual plan for the Baltic salmon stock and the fisheries exploiting that stock“ in August 2011 (European Commission 2011). With respect to genetic biodiversity the specific objective of this initiative is to ensure that the genetic integrity and diversity of the Baltic salmon stock is safeguarded and in this context “a phasing out of release of salmon in rivers with man made obstacles and without potential for re-establishment of self sustaining wild salmon populations in order to protect the genetic diversity of the wild stocks” (Explanatory memorandum of the proposal).

The proposal separates stocking from restocking. It suggests stocking may only be conducted in wild salmon rivers (Chapter IV, Article 12 of the proposal), and lists 28 such rivers in Annex 1 of the proposal (cf. Table 2 in this report). Restocking of rivers with potential for self-sustaining wild salmon populations should be supported according to the proposal provided that the release aims to establish or enhance a viable self sustaining wild population. Conservation and management measures must also be in place, including pre- and post-release monitoring programs (Chapter VI, Article 13). Further, the member state must provide information to the Commission including “for each wild salmon river stock, available genetic information” and “the activity of stocking and direct restocking of salmon” (Chapter IX, Article 23).

2.3 Objectives of the present study

The aim of this study is to summarize what is currently known regarding the genetic risks associated with large scale releases of salmon in the Baltic Sea. More specifically, we review and synthesize:

- current knowledge on gene level biodiversity of Atlantic salmon in the Baltic Sea (Chapter 5),
- information regarding compensatory releases in Sweden (number of salmon released, proportion marked/tagged individuals, origin of released salmon, etc.; Chapter 6),
- current knowledge regarding potential risks associated with large scale releases (Chapter 7),
- results from empirical studies of genetic effects of releases in salmonids (Chapter 7.1).

Further, we use previously published and unpublished data to address conservation genetic aspects associated with compensatory releases of salmon in the Baltic (Chapter 8).

3. Biology of the Atlantic salmon

Atlantic salmon occur on both sides of the Atlantic Ocean. In Europe, there are naturally reproducing salmon populations in rivers and streams from western Russia to Iceland and south to northern Spain (NRC 2002).

Most Atlantic salmon populations are anadromous (Jones 1959); individuals spend their first years in their natal river before migrating to the sea (or to a lake for landlocked populations) where they grow and become sexually mature (Klemetsen et al. 2003). During the sea ranging phase, different populations occur in a mixture and although populations from the same area migrate roughly to the same feeding grounds there is no tendency of close kin from the same river to aggregate (Koljonen et al. 2005; Palm et al. 2008; HELCOM 2011). Atlantic salmon spend one to several years in the sea before returning to the rivers to spawn.

Spawning takes place during fall and winter, and one individual can spawn several times with migrations to the sea between spawning events (Klemetsen et al. 2003). The Atlantic salmon is characterized by a strong instinct to return to their natal river or stream to spawn (so-called homing behaviour; Stabell 1984; Hansen et al. 1993). Although the homing behaviour is not fully perfect - some individuals stray to nearby rivers resulting in gene flow between populations of different rivers – this provides an opportunity for the salmon to genetically adapt to environmental conditions in their natal streams (e.g. Allendorf & Ryman 1987). Homing also results in the potential for relatively large genetic differences to occur over short geographical distances both within and among rivers (see review by Fraser et al. 2011). This in turn, means that a relatively large part of the genetic biodiversity of salmon is represented by genetic differences between individual populations. Losing individual populations thus can result in loss of a distinct part of the species gene pool that might represent a unique adaptation to a particular local environment (Allendorf & Luikart 2007).

3.1 Threat status of the Baltic salmon

The largest interference with Baltic salmon populations is the construction of water power plant stations, obstructing the route to spawning grounds (McCormick et al. 1998). Due to such constructions Atlantic salmon in the Baltic Sea is classified as Endangered (EN) according to the IUCN red list criteria although nationally, red list categories of salmon vary between Baltic Sea countries (Table 1; HELCOM 2007).

Atlantic salmon is included on the list of threatened and/or declining species and habitats of the Convention for the Protection of the marine Environment of the North-East Atlantic – the OSPAR Convention (OSPAR 2008, 2010) and on the Annexes II and V of the EU Habitats Directive (at present only in freshwater habitats). Atlantic salmon in the Baltic is recognized as a high priority species of global importance by the Helsinki Commission (HELCOM), the governing body of the Convention on the Protection of the Marine Environment of the Baltic Sea Area (also known as the Helsinki Convention; HELCOM 2007).

Table 1. IUCN threat status classification in national red lists.

Salmon IUCN threat status	**Country**	**Reference**
Critically endangered (CR)	Poland	www.helcom.fi
Endangered (EN)	Denmark, Estonia, Finland, Germany	Rassi et al. 2010; http://elurikkus.ut.ee; www.helcom.fi
Least concern (LC)	Sweden	Gärdenfors 2010
Unclear	Latvia, Lithuania, Russia	

Historically, 84 rivers flowing into the Baltic Sea have harbored Atlantic salmon populations. Currently, only 10 of these maintain self sustaining wild natural populations in safe numbers (Figure 1). Seven of these rivers are located in Sweden (Table 2; Figure 1), one at the Swedish-Finnish boarder (River Torneälven/Tornionjoki) and one each in Finland (River Simojoki), Latvia (River Salaca), and Lithuania (River Nemunas). The European Commission classifies 27 of the 84 rivers as “wild salmon rivers” (Table 2; European Commission 2011).

Of current wild salmon smolt production, 90% is produced in Swedish rivers (River Torneälven included; ICES 2011). Hatchery produced and released salmon is estimated to constitute about 70% of the salmon in the Baltic Sea (ICES 2011), while just a few years ago 90% of Baltic salmon originated from hatcheries (ICES 2003)

Table 2. Classification of Baltic salmon populations in separate rivers on a country by country basis from the Coalition Clean Baltic (Figure 1) and the European Commission (European Commission 2011), respectively.

Country	**Wild salmon rivers with populations in safe numbers (CCB classification)**	**Wild salmon rivers (EU classification)**
Belarus	0	0
Denmark	0	0
Estonia	0	Pärnu, Kunda, Keila, Vasalemma
Finland	Torneälven/Tornionjoki (shared with Sweden)	Torneälven/Tornionjoki (shared with Sweden)
Germany	0	0
Latvia	Salaca	Salaca, Vitrupe, Peterupe, Irbe, Uzava, Saka, Barta/Bartuva (shared with Lithuania)
Lithuania	Nemunas	Nemunas, Barta/Bartuva (shared with Latvia)
Poland	0	0
Russia	0	- (not a member of the EU)
Sweden	Kalixälven, Piteälven, Åbyälven, Byskeälven, Vindelälven, Ljungan, Emån Torneälven/Tornionjoki (shared with Finland)	Kalixälven, Råneälven, Piteälven, Åbyälven, Byskeälven, Rickleån, Sävarån, Ume/Vindelälven, Öreälven, Lögdeälven, Emån, Mörrumsån, Ljungan Torneälven/Tornionjoki (shared with Finland)

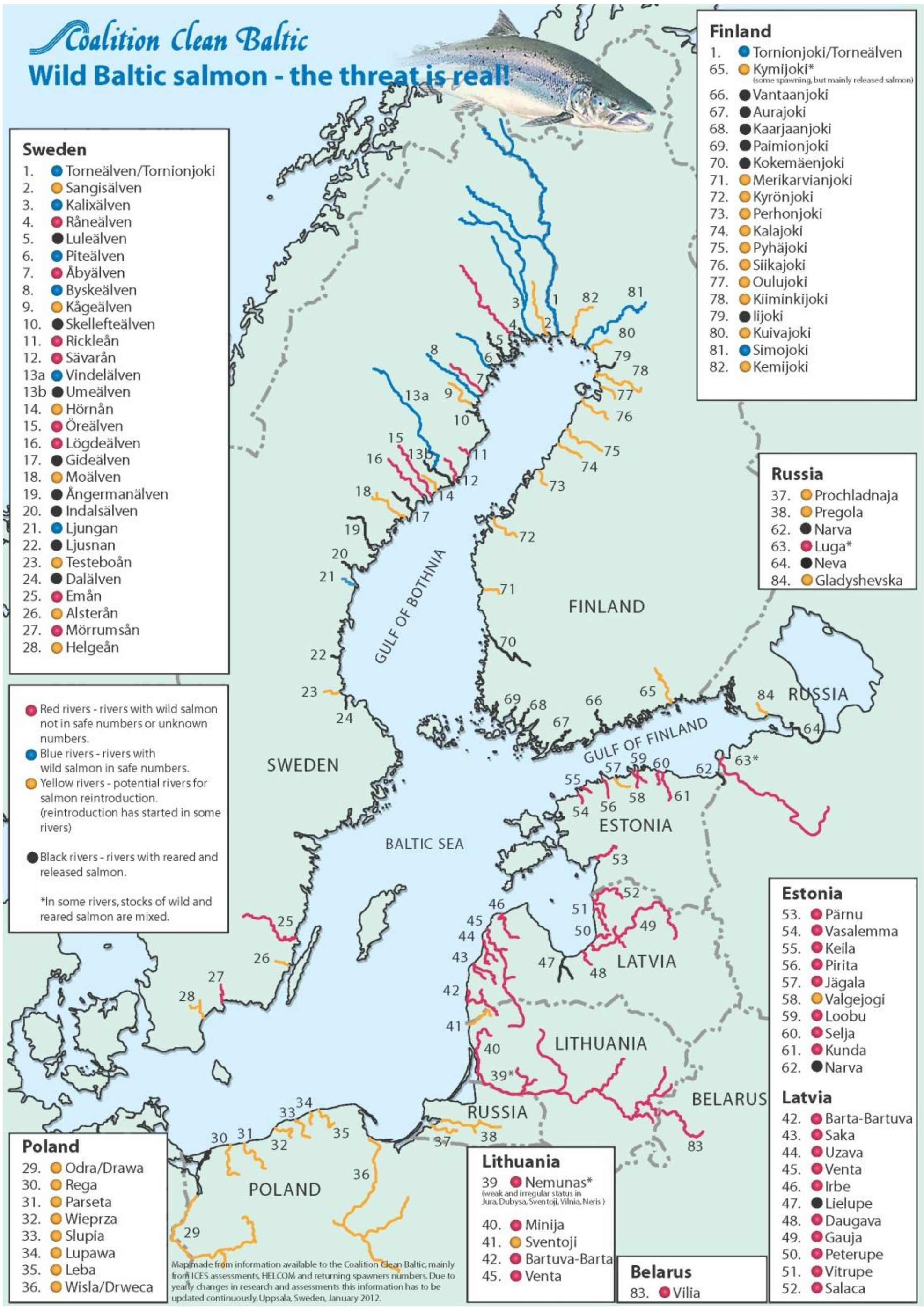


Figure 1. Baltic salmon rivers. The map is reproduced with kind permission from Coalition Clean Baltic (CCB 2012).

4. Exploitation and management of Baltic salmon

Atlantic salmon is important for commercial and recreational fishery in the Baltic area. To maintain or increase commercial and sport fishery, and to compensate for lost natural reproduction due to power plant constructions, substantial numbers of hatchery reared salmon are released every year. In Sweden, releases include permissions by local authorities for improving sport fisheries (and/or for conservation purposes) as well as large scale compensatory releases of fish for production losses caused by hydropower developments (Laikre & Palmé 2005; Laikre et al. 2006).

4.1 ICES assessment units

There is a general consensus that salmon in the Baltic Sea should be managed on a population level, i.e. on a river by river basis (Ståhl 1987; Koljonen et al. 1999; Verspoor et al. 1999; 2005; HELCOM 2011). The International Council for the Exploration of the Sea (ICES) has established six different assessment units for the Baltic Sea. These assessment units are:

1. *Northeastern Bothnian Bay stocks*, from River Perhonjoki to River Råneälven.
2. *Western Bothnian Bay stocks*, from River Lögdeälven to River Luleälven.
3. *Bothnian Sea stocks*, from River Dalälven to River Gideälven in Sweden, and from River Paimionjoki to River Kyrönjoki in Finland.
4. Western Main Basin stocks.
5. *Eastern Main Basin stocks*, i.e. stocks in Estonian, Latvian and Lithuanian rivers.
6. Gulf of Finland stocks.

The grouping of Baltic rivers into assessment units is based on management objectives as well as biological and genetic characteristics of the populations (ICES 2011). The units make sense from a management perspective; stocks of a particular unit are believed to exhibit similar migration patterns and it can be assumed that they are subjected to the same fisheries, experience the same exploitation rates and are affected by management in the same way. The genetic variability between stocks of an assessment unit is smaller than the genetic variability between stocks of different units (ICES 2011).

4.2 Mixed fishery

Harvest at feeding grounds means that it is not possible to separate which populations are included in the harvest – a so-called mixed fishery. Open Sea fishery in the Baltic Sea usually includes salmon from several assessment units in the same catch (ICES 2011). If mixed fishery is carried out indiscriminately, there is a risk of weak populations being over-fished and possibly extirpated (Laikre et al. 2005; Allendorf et al. 2008). To distinguish which populations are included in catches from mixed fisheries genetic analyses in combination with statistical approaches can be used (Pella & Milner 1987). Mixed fishery analyses represent a frequently used management tool in e.g., USA and Canada (Utter & Ryman 1993; Shaklee et al. 1999; Beacham et al. 2004; Flannery et al. 2010) but which has only to a limited extent been applied in Baltic waters using both genetic and life history data (e.g. Koljonen & McKinnel 1996; Koljonen & Pella 1997; Koljonen et al. 2005; Anderson et al. 2008).

At least until 2009, genetic data on catch composition was not used in salmon stock assessment in the Baltic Sea (ICES 2009). Rather, catch composition analyses in the Baltic have been focused on estimating proportions of wild fish, and hatchery fish from Finland and Sweden respectively (ICES 2011).

Of the total salmon catches in Sweden 2010 (418 tonnes), 39% represented offshore catches with an obvious risk of mixed fishery. River catches, which focuses directly on populations of individual rivers only represented 17%, whereas coastal catches represented 44% (ICES 2011). However, in 2011, the Swedish Agency for Water and Management (SwAM) decided to forbid offshore fishery with longline (*In Swedish: drivande linor med krok*) to 2013 (anchored floating gillnets (*In Swedish: svajgarn)* are already forbidden). The Swedish quota will instead only include river and coastal fisheries using traps (push-up traps and hoop nets (*In Swedish: ryssja*)) close to river mouths. During 2012, it is still allowed to take 40% of the Swedish quota of 34 327 salmon with longline, while 60% is earmarked for coastal fisheries with permanent fishing gears. There are intentions for the future to introduce similar regulations for the commercial trolling fishery at sea (Peter Funegård, SwAM, pers. comm.). Sport fisheries in rivers is outside national quotas, and sport fishermen have only a one fish daily bag limit during the annual time period when fishing is allowed in rivers.

Finland is the only other country besides Sweden in the Baltic region that has taking action in the same direction, however they allow fishing with longline for 4 000 salmon per year at maximum (of their total national quota of 31 667 salmon).

5. Current knowledge on genetic biodiversity of Baltic salmon

The first population genetic structure studies of Atlantic salmon were carried out in the early 1970s (e.g. Møller 1970; Payne et al. 1971; Behnke 1972; Payne 1974; Child et al. 1976). These studies, focusing on North American populations and using only single loci, indicated genetic sub structuring within the species. The methodology for analyzing several loci of Atlantic salmon providing opportunities to estimate of level of variation within and between populations was developed in the late 1970s using salmon from the British Isles (Cross & Ward 1980). The first study that involved some samples from Baltic waters was based on one single locus and focused only on genetic differences between European and North American salmon (Nyman & Pippy 1972). However, variation between Baltic and other European samples or variation within the Baltic Sea was not considered until later.

5.1 Literature review

To obtain information on what is currently known regarding genetic composition and spatio-temporal patterns of the Baltic salmon we searched the literature using the database Science Citation Index (ISI Web of Science) and Google Scholar, as well as compiling non-scientific publications ("gray literature"). As search criteria for scientific publications we used the following strings:

- genetic AND (differen* OR structure OR divergen*) AND Baltic in ISI Web of Science database
- genetic AND Salmo salar AND Baltic in the ISI Web of Science database
- genetic AND Salmo salar AND Baltic in Google Scholar.

A total of 37 scientific studies, based multiple nuclear loci and/or mitochondrial DNA information, delineating patterns of Baltic salmon genetic diversity have been identified. "Gray" literature of Swedish salmon population comprises seven additional reports. Out of these 44, the 36 studies presenting data on number of individuals genotyped are summarized in Table 3a and b. In total, they cover genetic information from populations representing 35 Baltic river systems (Rivers Umeälven and Vindelälven counted separately), and c. 23 000 genotyped individuals.

It is difficult to construct search criteria that result in a completely exhaustive retrieval, and we do not claim that the present bibliography includes each and every study on genetic variability on Baltic salmon. We believe, however, that most of the scientifically published work including Baltic salmon samples is included here.

5.1.1 Early genetic studies of Baltic salmon

Different Swedish salmon stocks were described in the late 1970’s based on tagging data (Larsson et al. 1979). Dr. Gunnar Ståhl, Stockholm University, carried out the first multi-locus studies of Baltic salmon demonstrating strong substructuring and low levels of migration between natural Baltic populations (Ståhl 1981). During the 1980s Ståhl showed that:

- Atlantic salmon is naturally substructured into multiple genetically differentiated and more or less reproductively isolated populations within as well as between major drainages (Ståhl 1981, 1987).
- The genetic variation over the entire species range is divided into three major clusters – the western Atlantic, the eastern Atlantic and the Baltic (Ståhl 1987).
- The greatest genetic difference is found between populations from the North America vs. Europe. This difference is twice as great as that between major clusters within Europe, i.e. Baltic vs. eastern Atlantic (Ståhl 1987).
- Hatchery stocks exhibit lower levels of genetic variation than the wild populations they originate from (Ståhl 1983).
- Large allele frequency changes occur between age classes in hatcheries indicating low number of parents to offspring produced for release (Ståhl 1983).
- The pattern of genetic differentiation between hatchery stocks differs from that for natural populations. The major reason for the observed differences between hatchery and wild stocks is suggested to be the use of too few parents in hatchery production (Ståhl 1987).

The results from Ståhl´s studies had several implications for conservation genetic management which were pointed out early (Ståhl 1981; Ryman 1981; Ryman 1983; Ståhl 1987) but which were largely ignored at that time. It was not until the late 1980s (Koljonen 1989) and the late 1990s that other researchers continued the population genetic studies of Baltic salmon that Ståhl initiated (Table 3a and b).

5.1.2 Genetic uniqueness of Baltic salmon

Later studies have confirmed Ståhl´s work in the 1980s showing genetic uniqueness of Baltic salmon compared to other population in Atlantic waters (e.g. Verspoor et al. 1999, 2005; Nilsson et al. 2001; Koljonen et al. 2002; Johannesson & André 2006). The genetic distinctness of Baltic salmon populations is maintained through low migration rates through the Danish Belts (between the Baltic Sea and the Atlantic Ocean; Klemetsen et al. 2003). Further, Baltic salmon populations exhibit lower genetic variation than other Atlantic populations. This is probably due to bottleneck events at the colonization of the Baltic Sea area after the last ice age, or because of small population sizes during time in glacial refugia (Ståhl 1987; Verspoor 1997; Verspoor et al. 1999; Nilsson et al. 2001; Langefors 2005; Johannesson & André 2006; Johannesson et al. 2011).

5.1.3 Differentiation patterns within the Baltic Sea

The clear genetic divergence pattern among Baltic salmon populations shown by Ståhl (1981, 1987) has been further explored in a number of studies. Strong homing behavior in Atlantic salmon results in a clear and temporally stable differentiation pattern, where each Baltic salmon river harbor at least one genetically unique population (Nilsson 1997; Koljonen et al. 2002; Verspoor et al. 2005; Ozerov et al. 2010). Genetic structuring within river systems has been observed in the Rivers Torneälven and Kalixälven (Ståhl 1987; Lohm 2002). Occasional straying occurs mostly among geographically proximate populations resulting in an association between genetic and geographic distance (isolation by distance; Bourke et al. 1997; Koljonen et al. 1999; Vasemägi et al. 2001). Thus, genetic diversity in one population can to some degree depend on other geographically close populations (Vasemägi et al. 2005a).

5.1.4 Genetic variation within Baltic populations

Wild populations of Atlantic salmon are assumed to be genetically temporally stable (Ståhl 1987; Verspoor et al. 2005). This has been shown also for Baltic salmon specifically (Koljonen 1989) and when temporally separated samples from the same locality have been available they have most often been pooled together in genetic analyses. However, some studies have shown temporal heterogeneity in samples from hatchery stocks (Ståhl 1987; Säisä et al. 2003; Verspoor et al. 2005). Present day hatchery stocks have lost genetic diversity compared to wild populations, and are also genetically diverged from the wild populations they are meant to represent (Ståhl 1983; Säisä et al. 2003).

Effective population size (N_e; Wright 1969, p. 211) determines the rate of loss of genetic variation. We have found no estimates on effective population size for wild salmon populations in the Baltic Sea. Genetic data appears to have been used only twice to estimate N_e of salmon in the Baltic region and those studies involved brood stocks (Koljonen 2002; Säisä 2003).

5.1.5 Evolutionary history of Baltic salmon

On a higher hierarchical level there is a genetic substructuring of the total Baltic population, where northern, southern, and eastern salmon populations form different genetic groups (Koljonen et al. 1999; Säisä et al. 2005). This is most likely due to colonization of the Baltic Sea after the last ice age of two or more phylogeographic lineages, surviving the ice age in different glacial refugia (Koljonen et al. 1999; Nilsson et al. 2001; Säisä et al. 2005).

Exact routes of colonization and location of glacial refugia are under debate (Nilsson et al. 2001; Tonteri et al. 2007), but most authors agree on one freshwater refugium being located east or south of the ice sheath covering the whole area of the Baltic Sea during the last glaciation. As the ice retreated salmon from this southern or eastern refugium migrated into the Baltic Sea area, and made up the southern and eastern populations in the present Baltic Sea (Koljonen et al. 1999; Nilsson et al. 2001; Säisä et al. 2005).

A possible colonization route for the populations in present day Bothnian Bay is from the Atlantic Ocean over the “Närke Strait”, a passage between the Baltic Sea and the Atlantic Ocean opening between 10 300 and 9 500 years B.P. (Koljonen et al. 1999; Säisä et al. 2005). Genetic similarities between populations in the Bothnian Bay and around Iceland could be explained by this colonization route (Verspoor et al. 1999). The theory of an Atlantic glacial refugium has been questioned, however, and it is possible that also populations in the northern part of the Baltic Sea colonized the area from the east (Nilsson et al. 2001). Possibly an additional third phylogeographic lineage colonized the Baltic Sea from a southern refugium, making up present populations in the southernmost Baltic (Säisä et al. 2005).

Table 3a. Genetic information regarding salmon rivers flowing into the Baltic. The information originates from scientific literature and includes 35 Baltic rivers. Studies providing at least origin and number of salmon samples were included in this table. H=hatchery, W=wild, B=both hatchery and wild, and U=unknown origin. H_e = expected heterozygosity, H_o = observed heterozygosity, h = haplotype/gene diversity. Data included in more than one scientific publication were included from the original study, but all of the other found publications are mentioned as references. Sometimes it was hard to identify reuse of samples, meaning that duplicates of individuals may exist in this synthesis.

River system	**River system number (Figure 1)**	**River**	**Country**	**Sampling years**	**H/W**	**Markers**	**Approx. number of ind.**	H_e	H_o	h	**References**
Byskeälven	8	Byskeälven	Sweden	1999	W	mtDNA	53			0.073	Nilsson et al. 2001
				1979 1980 1994	W	Allozymes	188	0.035 - 0.183			Koljonen & McKinnel 1996; Koljonen & Pella 1997; Koljonen et al. 1999; Ryman & Ståhl 1981; Ståhl 1981, 1983, 1987
				2003	W	Microsatellites	184	0.760			Koljonen 2006; Säisä et al. 2005
				1980	H	Allozymes	40	0.018			Ståhl 1983, 1987
Dalälven	24	Dalälven	Sweden	1997 1998	B	mtDNA	100			0.167	Nilsson et al. 2001;
				1995	H	mtDNA	50			0.000	Verspoor et al. 1999
				1994 1999		Microsatellites	100	0.522 - 0.730			Koljonen 2006; Langefors 2005; Säisä et al. 2005

Table 3a cont.

River system	River system number (Figure 1)	River	Country	Sampling years	H/W	Markers	Approx. number of ind.	H_e	H_o	h	References
Dalälven cont.	24	Dalälven cont.	Sweden	1988 1993	H	Allozymes	250	0.045	0.078		Bourke et al. 1997; Koljonen & McKinnel 1996; Koljonen & Pella 1997; Koljonen et al. 1999
				1994	H	MHC IIB RFLP/DGGE	40	0.870			Langefors 2005
				1994		Sequenced MHC IIB					Langefors et al. 2001
				1994		MHC IIB RFLP	41	0.810	0.830		Langefors et al. 1998
Daugava	48	Daugava	Latvia	1998	B	mtDNA	53			0.000	Nilsson et al. 2001
				1996	H	Allozymes	125	0.051			Koljonen et al. 1999
				1996	H	Microsatellites	70	0.700			Koljonen 2006; Säisä et al. 2005

Table 3a cont.

River system	River system number (Figure 1)	River	Country	Sampling years	H/W	Markers	Approx. number of ind.	H_e	H_o	h	References
Emån	25	Emån	Sweden	1998 1999	W	mtDNA	59			0.000	Nilsson et al. 2001
				1999 2003	W	Microsatellites	163	0.730			Koljonen 2006; Säisä et al. 2005
				1981	H	Allozymes	82	0.015			Ståhl 1983
Gauja	49	Gauja	Latvia	1996	W	Microsatellites	70	0.680			Koljonen 2006; Säisä et al. 2005
Iijoki	79	Iijoki	Finland	1981 1986 1987 1990 1993 1997	H	Allozymes	594	0.030 - 0.180	0.034		Koljonen 1995; Koljonen & McKinnel 1996; Koljonen & Pella 1997; Koljonen et al. 1989; Koljonen et al. 1999;
				1973 1980 1992 1995 1997 1999	H	Microsatellites	512	0.672 - 0.679			Koljonen 2006; Koljonen et al. 2002; Säisä et al. 2003; Säisä et al. 2005; Vasemägi et al. 2005b

Table 3a cont.

River system	River system number (Figure 1)	River	Country	Sampling years	H/W	Markers	Approx. number of ind.	H_e	H_o	h	References
Iijoki cont.	79	Iijoki cont.	Finland	1962	W	Microsatellites	70	0.680			Koljonen et al. 2002; Säisä et al. 2003; Säisä et al. 2005
				1997 1999	H	mtDNA	15				Vasemägi et al. 2005b
Indalsälven	20	Indalsälven	Sweden	1995 1997	H	mtDNA	149			0.536	Nilsson et al. 2001; Vasemägi et al. 2005b
				1979 1980 1993	H	Allozymes	355	0.017 - 0.042			Koljonen & McKinnel 1996; Koljonen & Pella 1997; Koljonen et al. 1999; Ryman & Ståhl 1981; Ståhl 1983, 1987
				1995 1997	H	Microsatellites	129	0.740			Koljonen 2006; Säisä et al. 2005; Vasemägi et al. 2005b

Table 3a cont.

River system	River system number (Figure 1)	River	Country	Sampling years	H/W	Markers	Approx. number of ind.	H_e	H_o	*h*	References
Kalixälven	3	Kalixälven	Sweden	1989	W	mtDNA	35			0.363	Nilsson et al. 2001
				1979 1981 1987-1989		Allozymes	1124	0.059 -0184			Koljonen & McKinnel 1996; Koljonen & Pella 1997; Koljonen et al. 1999; Ryman & Ståhl 1981; Ståhl 1981, 1983, 1987
					W	Microsatellites	226	0.710			Koljonen 2006; Säisä et al. 2005
		Kaitumälven		1979	W	Allozymes	98	0.030			Ryman & Ståhl 1981; Ståhl 1981, 1983, 1987
		Ängesån Satter		1981	W	Allozymes	46	0.026			Ståhl 1983, 1987
		Ängesån Vettasjoki		1981	W	Allozymes	79	0.026			Ståhl 1983, 1987
		Ängesån Vaitiojoki		1981	W	Allozymes	29	0.031			Ståhl 1983, 1987

Table 3a cont.

River system	**River system number (Figure 1)**	**River**	**Country**	**Sampling years**	**H/W**	**Markers**	**Approx. number of ind.**	H_e	H_o	h	**References**
Keila	55	Keila	Estonia	1996 1997	W	mtDNA	59			0.000	Nilsson et al. 2001
				1996 2000	W	Microsatellites Minisatellites	117	0.678	0.631		Vasemägi et al. 2005a
				1994 1995	W	Allozymes	63	0.077			Koljonen et al. 1999
				1997	W	Microsatellites	53	0.690			Koljonen 2006; Säisä et al. 2005;
Kemijoki	82	Kemijoki	Finland	1981 1983 1988 1992	H	Allozymes	559	0.040 - 0.163	0.044		Koljonen 1989; Koljonen 1995; Koljonen & McKinnel 1996; Koljonen & Pella 1997
Kunda	61	Kunda	Estonia	1996 1997	W	mtDNA	48			0.034	Nilsson et al. 2001
				1996-1998	W	Microsatellites Minisatellites	91	0.596	0.642		Vasemägi et al. 2005a
				1994 1995	W	Allozymes	59	0.078			Koljonen et al. 1999
				1996 1999-2007	W	Microsatellites	101	0.610 - 0.630	0.620		Koljonen 2006; Ozerov et al. 2010; Säisä et al. 2005

Table 3a cont.

River system	River system number (Figure 1)	River	Country	Sampling years	H/W	Markers	Approx. number of ind.	H_e	H_o	*h*	References
Kymijoki	65	Kymijoki	Finland	1981-1983		Allozymes	60	0.040	0.035		Koljonen 1989
Ljungan	21	Ljungan	Sweden	1997 1998	B	mtDNA	49			0.594	Nilsson et al. 2001
				1996	W	Allozymes	52	0.062			Koljonen et al. 1999
				1998 2003	W	Microsatellites	133	0.770			Koljonen 2006; Säisä et al. 2005
Ljusnan	22	Ljusnan	Sweden	1997 1998	H	mtDNA	101			0.077	Nilsson et al. 2001; Vasemägi et al. 2005b
				1993	H	Allozymes	50	0.057			Koljonen & McKinnel 1996; Koljonen & Pella 1997; Koljonen et al. 1999
				1997-1999	H	Microsatellites	103	0.740			Koljonen 2006; Säisä et al. 2005; Vasemägi et al. 2005b
Loobu	59	Loobu	Estonia	1996 1999	W	Microsatellites Minisatellites	79	0.530 - 0.532	0.542 - 0.663		Vasemägi et al. 2005a
				1994 1995	W	Allozymes	50	0.068			Koljonen et al. 1999

Table 3a cont.

River system	River system number (Figure 1)	River	Country	Sampling years	H/W	Markers	Approx. number of ind.	H_e	H_o	h	References
Luga	63		Russia	2003		Microsatellites	67				Koljonen 2006
Luleälven	5	Luleälven	Sweden	1995 1997	H	mtDNA	206			0.376 - 0.439	Nilsson et al. 2001; Verspoor et al. 1999; Vasemägi et al. 2005b
				1981 1993	H	Allozymes	140	0.025-0.056	0.094		Bourke et al. 1997; Koljonen & McKinnel 1996; Koljonen & Pella 1997; Koljonen et al. 1999; Ståhl 1983, 1987;
				1995	H	MHC IIB RFLP/DGGE	38	0.861			Langefors 2005
				1995	H	Sequenced MHC IIB					Langefors et al. 2001
				1995	H	MHC IIB RFLP	36	0.810	0.860		Langefors et al. 1998
				1995 1997	H	Microsatellites	158	0.523-0.760			Koljonen 2006; Langefors 2005; Säisä et al. 2005; Vasemägi et al. 2005b

Table 3a cont.

River system	River system number (Figure 1)	River	Country	Sampling years	H/W	Markers	Approx. number of ind.	H_e	H_o	h	References
Lögdeälven	16	Lögdeälven	Sweden	1994 1995	W	mtDNA	43			0.047	Nilsson et al. 2001
				1995	W	Microsatellites Minisatellites	49	0.772	0.774		Vasemägi et al. 2005a
				1979	W	Allozymes	69	0.047			Koljonen & McKinnel 1996; Koljonen & Pella 1997; Koljonen et al. 1999; Ryman & Ståhl 1981; Ståhl 1981, 1983, 1987
				1995 2003	W	Microsatellites	99	0.730			Koljonen 2006; Säisä et al. 2005
Mörrumsån	27	Mörrumsån	Sweden	1996	W	mtDNA	51			0.000	Nilsson et al. 2001
				1994	W	Allozymes	67	0.082			Koljonen et al. 1999
						MHC IIB RFLP/DGGE	46	0.645			Langefors 2005
				1993 2003	W	Microsatellites	227	0.560-0.720			Langefors 2005; Säisä et al. 2005
				1993		Sequenced MHC IIB					Langefors et al. 2001
				1993		MHC IIB RFLP	13	0.630	0.690		Langefors et al. 1998

Table 3a cont.

River system	**River system number (Figure 1)**	**River**	**Country**	**Sampling years**	**H/W**	**Markers**	**Approx. number of ind.**	***H_e***	***H_o***	***h***	**References**
Narva	62	Narva	Estonia/ Russia	1998 2000	H	Microsatellites Minisatellites	54	0.722	0.717		Vasemägi et al. 2005a
				1999 2001	H	Microsatellites	110	0.670	0.660		Koljonen 2006; Ozerov et al. 2010
Neva	64	Neva	Russia	1995	H	mtDNA	45			0.087	Nilsson et al. 2001
				1999-2007	H	Microsatellites	397	0.600 - 0.750	0.630 - 0.735		Koljonen et al. 2002; Koljonen 2006; Ozerov et al. 2010; Ryynänen et al. 2007; Säisä et al. 2005; Tonteri et al. 2005; Tonteri et al. 2007;
				1996 1998	H	Microsatellites Minisatellites	70	0.733 - 0.761	0.724 - 0.745		Vasemägi et al. 2005a
				1990 1993 1995 1997	W	Allozymes	370	0.064			Koljonen 1995; Koljonen & McKinnel 1996;Koljonen & Pella 1997; Koljonen et al. 1999; Tonteri et al. 2005

Table 3a cont.

River system	River system number (Figure 1)	River	Country	Sampling years	H/W	Markers	Approx. number of ind.	H_e	H_o	*h*	References
Neva cont.	64	Neva cont.	Russia		H	SNP	42	0.180	0.180		Ryynänen et al. 2007
				1983	H	Allozymes	261	0.044	0.041		Koljonen 1989
		Neva (Laukaa, Finland)		1981	H	Allozymes	70	0.037	0.043		Koljonen 1989
Oulujoki	77	Oulujoki	Finland	1981 1992 1997	H	Allozymes	288	0.058-0.076	0.056		Koljonen 1989; Koljonen 1995; Koljonen & McKinnel 1996; Koljonen & Pella 1997; Koljonen et al. 1999
						Allozymes	180				Koljonen & McKinnel 1996; Koljonen & Pella 1997
				1940	W	Microsatellites	69	0.730			Säisä et al. 2003
				1995 1997	H	Microsatellites	227	0.660-0.682			Koljonen 2006; Koljonen et al. 2002; Säisä et al. 2003; Säisä et al. 2005; Vasemägi et al. 2005b
					H	mtDNA	58				Vasemägi et al. 2005b

Table 3a cont.

River system	River system number (Figure 1)	River	Country	Sampling years	H/W	Markers	Approx. number of ind.	H_e	H_o	*h*	References
Pärnu	53	Pärnu	Estonia	1997	W	mtDNA	23			0.000	Nilsson et al. 2001
				1997	W	Microsatellites	26	0.710			Koljonen 2006; Säisä et al. 2005;
Råneälven	4	Råneälven	Sweden	2003	W	Microsatellites	35				Koljonen 2006
Simojoki	81	Simojoki	Finland	1981-1983 1992 1993 1995	W	Allozymes	975	0.048 - 0.064	0.044 - 0.083		Bourke et al. 1997; Koljonen 1989; Koljonen 1995; Koljonen & McKinnel 1996;Koljonen & Pella 1997; Koljonen et al. 1999
				1997	W	Microsatellites	139	0.700			Koljonen et al. 2002; Säisä et al. 2005; Koljonen 2006
				1995		mtDNA	50			0.041	Verspoor et al. 1999

Table 3a cont.

River system	River system number (Figure 1)	River	Country	Sampling years	H/W	Markers	Approx. number of ind.	H_e	H_o	h	References
Skellefteälven	10	Skellefteälven	Sweden	1995 1996	H	mtDNA	191			0.440 - 0.463	Nilsson 1997; Nilsson et al. 2001; Vasemägi et al. 2005b
				1996	H	Microsatellites Minisatellites	52	0.726	0.722		Vasemägi et al. 2005a
				1995 1996	H	Microsatellites	202	0.498 - 0.700			Koljonen 2006; Nilsson 1997; Säisä et al. 2005; Vasemägi et al. 2005b
				1993	H	Allozymes	434	0.020 - 0.046			Koljonen & McKinnel 1996; Koljonen & Pella 1997; Koljonen et al. 1999; Ståhl 1983, 1987
Sävarån	12	Sävarån	Sweden	2005 2006	W	Microsatellites	98	0.726	0.727		Nilsson et al. 2008

Table 3a cont.

River system	River system number (Figure 1)	River	Country	Sampling years	H/W	Markers	Approx. number of ind.	H_e	H_o	*h*	References
Torneälven	1	Torneälven	Finland/ Sweden	1979-2000	W	Allozymes	846	0.061	0.023 - 0.074		Bourke et al. 1997; Koljonen & McKinnel 1996; Koljonen & Pella 1997; Koljonen et al. 1999; Ryman & Ståhl 1981; Ståhl 1981, 1983, 1987
				1989 1994 1995	W	mtDNA	185			0.115 - 0.220	Nilsson et al. 2001; Verspoor et al. 1999
					W	SNP	36	0.150	0.150		Ryynänen et al. 2007
					W	Sequenced GH1 gene					Ryynänen & Primmer 2004
				2000	W	Microsatellites	219	0.590 - 0.712	0.590 - 0.600		Koljonen 2006; Koljonen et al. 2002; Ryynänen et al. 2007; Tonteri et al. 2005, 2007

Table 3a cont.

River system	River system number (Figure 1)	River	Country	Sampling years	H/W	Markers	Approx. number of ind.	H_e	H_o	h	References
Torneälven cont.	1	Torneälven cont.	Finland/ Sweden	1992 1993	H	Allozymes	629	0.047	0.080		Bourke et al. 1997; Koljonen & McKinnel 1996; Koljonen & Pella 1997; Koljonen et al. 1999
					H	Microsatellites	179	0.702			Koljonen 2006; Koljonen et al. 2002
					B	Microsatellites	61				Vasemägi et al. 2005b
					B	mtDNA	61				Vasemägi et al. 2005b
				1981 1992	B	Allozymes	380	0.048	0.053		Koljonen 1989; Koljonen 1995
					U	Microsatellites Minisatellites	36	0.520	0.500		Tonteri et al. 2010
		Lainio		1979	W	Allozymes	14		0.027		Ryman & Ståhl 1981; Ståhl 1981, 1983, 1987
		Kukkola		1980	H	Allozymes	50		0.031		Ryman & Ståhl 1981; Ståhl 1983, 1987
		Mouth of Torneälven		1980	H	Allozymes	130		0.027		Ståhl 1983, 1987

Table 3a cont.

River system	River system number (Figure 1)	River	Country	Sampling years	H/W	Markers	Approx. number of ind.	H_e	H_o	*h*	References
Umeälven	13b	Umeälven	Sweden	1992 1995 2002	H	mtDNA	184			0.527	Nilsson et al. 2001; Vasemägi et al. 2005b
				1994 1995 2002	H	Microsatellites	191	0.473-0.650			Koljonen 2006; Langefors 2005; Säisä et al. 2005; Vasemägi et al. 2005b
				1995	H	Microsatellites Minisatellites	50	0.674	0.680		Vasemägi et al. 2005a
				1989 1990		Allozymes	296	0.030-0.104			Koljonen & McKinnel 1996; Koljonen & Pella 1997; Koljonen et al. 1999
				1994	H	MHC IIB RFLP/DGGE	45	0.684			Langefors 2005
						Sequenced MHC IIB	45				Langefors et al. 2001
						MHC IIB RFLP	26	0.500	0.420		Langefors et al. 1998
Vasalemma	54	Vasalemma	Estonia	1996 1997	W	mtDNA	27			0.000	Nilsson et al. 2001
				1994 1995	W	Allozymes	43	0.071			Koljonen et al. 1999

Table 3a cont.

River system	**River system number (Figure 1)**	**River**	**Country**	**Sampling years**	**H/W**	**Markers**	**Approx. number of ind.**	H_e	H_o	h	**References**
Venta	45	Venta	Latvia/ Lithuania	1996	W	Allozymes	94	0.060			Koljonen et al. 1999
					W	Microsatellites	66	0.700			Koljonen 2006; Säisä et al. 2005
Vindelälven	13a	Vindelälven	Sweden	1985-2003	W	mtDNA	481			0.430-0.464	Nilsson 1997; Nilsson et al. 2001; Vasemägi et al. 2005b
					W	SNP	44	0.120	0.100		Rynnänen et al. 2007
				1985-2003	W	Microsatellites	637	0.410-0.670	0.470		Koljonen 2006; Nilsson 1997; Ryynänen et al. 2007; Säisä et al. 2005; Tonteri et al. 2005; Tonteri et al. 2007; Vasemägi et al. 2005b
				1995	W	Microsatellites Minisatellites	50	0.668	0.678		Vasemägi et al. 2005a
				1989 1990		Allozymes	100	0.040			Koljonen & Pella 1997; Koljonen et al. 1999
					W	Microsatellites Minisatellites	37	0.490	0.470		Tonteri et al. 2010

Table 3a cont.

River system	River system number (Figure 1)	River	Country	Sampling years	H/W	Markers	Approx. number of ind.	H_e	H_o	h	References
Åbyälven	7	Åbyälven	Sweden	2003	W	Microsatellites	77				Koljonen 2006
Ångermanälven	19	Ångermanälven	Sweden	1995	H	mtDNA	184			0.480-0.491	Nilsson 1997; Nilsson et al. 2001; Vasemägi et al. 2005b
				1993	H	Allozymes	100	0.048			Koljonen & McKinnel 1996; Koljonen & Pella 1997; Koljonen et al. 1999
				1995	H	Microsatellites	168	0.493-0.750			Koljonen 2006; Nilsson 1997; Säisä et al. 2005; Vasemägi et al. 2005b
Öreälven	15	Öreälven	Sweden	2003	W	Microsatellites	25				Koljonen 2006

Table 3b. Genetic information regarding salmon rivers flowing into the Baltic. The information originates from "gray literature" and includes eleven Swedish rivers. H= hatchery and W= wild. H_e = expected heterozygosity, H_o = observed heterozygosity, *h* = haplotype/gene diversity. In order to avoid duplicating samples, individuals/results are mentioned in the earliest published report only. Data included in scientific publications before published in "gray" reports are not included in this table. These approaches were, however, sometimes hard to follow, meaning that duplicates of individuals may exist in this synthesis.

River system	**River system number (Figure 1 and 2)**	**River**	**Sampling years**	**Year classes**	**H/W**	**Type of marker**	**Approx. number of ind.**	H_e	H_o	*h*	**References**
Dalälven	24	Dalälven	1988 1993 1997	at least 1993 1996-1998	H	Allozymes	640	0.098-0.130			Jansson 1995; Jansson & Öst 1998; Öst & Jansson 2001
						mtDNA	155			0.160-0.170	
Indalsälven	20	Indalsälven	1987 1988 1990 1992 1997	at least 1987 1988 1992 1996	H	Allozymes	338	0.084-0.122			Jansson 1995; Öst & Jansson 1999, 2001
						mtDNA	74			0.520	
Kalixälven	3	Kalixälven	1987-1989	unknown	W	Allozymes	457	0.144			Jansson 1993, 1995
		Kaitumälven	1987-1989	unknown	W	Allozymes	239	0.143	0.150		Jansson 1993, 1995
		Ängesån	1987-1989	unknown	W	Allozymes	488	0.157-0.173	0.200		Jansson 1993, 1995

Table 3b cont.

River system	**River system number (Figure 1 and 2)**	**River**	**Sampling years**	**Year classes**	**H/W**	**Type of marker**	**Approx. number of ind.**	H_e	H_o	*h*	**References**
Ljungan	21	Ljungan	1986 1996 1998	at least 1995-1998	H/W	Allozymes	378	0.106 - 0.160			Jansson 1997; Öst & Jansson 1999, 2001
						mtDNA	49				
Ljusnan	22	Ljusnan	1992 1998	at least 1992 1997 1998	H	Allozymes	252	0.111 - 0.122		0.070	Jansson 1995; Öst & Jansson 1999, 2001
						mtDNA	51				
Luleälven	5	Luleälven	1992 1997	1992 1996	H	Allozymes	140	0.107 - 0.141		0.560	Jansson 1995; Öst & Jansson 2001
						mtDNA	38				
Mörrumsån	27	Mörrumsån	1994 1996	unknown	W	Allozymes	98				Jansson & Öst 1998
						mtDNA	51			0.000	
Skellefteälven	10	Skellefte-älven	1993 1994	at least 1993 1994	H	Allozymes	268	0.097 - 0.103		0.440	Jansson 1995; Öst & Jansson 2001
						mtDNA	50				

Table 3b cont.

River system	**River system number (Figure 1 and 2)**	**River**	**Sampling years**	**Year classes**	**H/W**	**Type of marker**	**Approx. number of ind.**	H_e	H_o	h	**References**
Torneälven	1	Lainioälven	unknown	unknown	W	mtDNA	14			0.480	Jansson & Öst 1998
		Torneälven	1988 1989	unknown	H/W	Allozymes	556	0.153	0.140 - 0.210		Jansson 1993, 1995
Umeälven	13b	Umeälven	1987 1988 1992 1993	1987-1992	H/W	Allozymes	398	0.075 - 0.160			Jansson 1997; Jansson & Öst 1998; Öst & Jansson 2001
						mtDNA	41			0.510-0.540	
Ångerman-älven	19	Ångerman-älven	1992	at least 1992	H	Allozymes	100	0.085 - 0.125			Jansson 1997; Jansson & Öst 1998, 2001
						mtDNA	63			0.490	

5.1.6 Available genotypic data and tissue archives on Baltic salmon

In total genotypic information is available from 35 of the 85 present or previous Baltic salmon rivers covering sampling years from the late 1970s to 2007. Including both scientific and non-scientific studies, more than 23 000 individual Baltic salmon have been genotyped. If the ICES WGBAST baseline data generated between 1995-2008 by Koljonen´s lab (parts of it already published in scientific peer review publications) is included this figure increase to almost 24 000 individuals. Presumably, this raw data is still accessible from the researchers that have carried out the studies (Table 3a and b).

The extent to which tissue or DNA archives exists that can be used for future genetic studies are available is not clear. The tissue bank at the Division of Population Genetics, Department of Zoology, Stockholm University comprises a total of 9 051 individual salmon, and SLU Department of Wildlife, Fish and Environmental Studies in Umeå has DNA samples from approximately 6 500 individual salmon. To our knowledge, no tissue samples have been saved from the research work done at the Swedish Salmon Research Institute in Älvkarleby (LFI; see Chapter 6.2). It is at the moment unclear to us if there are other research groups in the Baltic region that have access to tissue or DNA collections. Securing both existing genotypic databases and possible tissue and DNA archives are of vital importance for future genetic monitoring of Baltic salmon genetic biodiversity (Laikre et al. 2008; Jackson et al. 2012).

6. Large scale releases of salmon in the Swedish part of the Baltic Sea

Large scale releases of Atlantic salmon and other salmonid fishes have been carried out for over a century more or less world wide (Laikre 1999 and references therein). Salmonid species including Atlantic salmon have also been introduced outside their native range, for instance to Chile which is now a world leading producer of salmon based exclusively on the introduction and farming of this non-native species (Gajardo & Laikre 2003).

Conservation genetic concerns about the effect of releases on native gene pools have been expressed by conservation and population geneticists since it has been possible to generate information on genetic differentiation and substructuring (Ryman 1981; Ryman & Ståhl 1981; Allendorf & Phelps 1981). In Baltic area releases of salmon have occurred since the 19th century. In this chapter we summarize the background, history and current knowledge on releases of Atlantic salmon in the Swedish part of the Baltic Sea.

6.1 Current salmon releases in Swedish waters

Stocking of salmon in Swedish waters is presently conducted for two purposes: *1*) to compensate for production loss caused by hydropower developments which prohibit natural migration of spawners to reproduction areas in rivers and migration of smolt to feeding areas in the Baltic, and *2*) to support weak natural populations to increase local harvest potential.

The amount of salmon to be released for compensating effects of hydropower plants and where geographically releases are to be conducted is determined by Swedish Water Court rulings. To perform the second type of release, permit from the local county administrative board is needed since 1955. During the period 1995-2001 95 such permits were issued of which 66 and 83 include information on released stock and number of fish, respectively (Laikre & Palmé 2005; Laikre et al. 2006). Compared to compensatory releases, salmon releases authorized by county administrative boards constitute only a minor fraction.

The intention of conservation releases is to cease as soon as the natural reproduction has reached acceptable levels. For instance, the River Dalälven salmon hatchery strain has been released into the River Testeboån to increase productivity of this river (Laikre et al. 2006; HELCOM 2011). For such conservation releases, pre-smoltificated salmon (larvae/fry and/or eggs) with low survival rate is often used (Jens Persson, SLU, pers. comm.), in contrast to compensatory measures where mostly smoltificated individuals are released.

6.2 History of compensatory releases in Sweden

Releases of salmon fry/larvae and smolt have occurred in Sweden since late 19th century (Öst & Jansson 1999). The first hydro electric stations were built in Sweden 1880s, and the Swedish Government's hydro power plant investment started in the early 1900s.

The first Swedish salmon hatchery was established in 1864 in River Umeälven, but when hydro power plants began to block migratory routes of salmon in late 1800 the first solution was to build fish ladders. However, in 1913 a proposal of rearing of smolt for release was put forward and was approved (Lindroth 1984).

Building of hydro power stations in larger salmon rivers in Sweden started in the 1940s. In 1945 an investigation group was established to give guidelines for compensatory measures with respect to migratory salmon. Their guidelines were presented in 1951 and included that *i*) compensatory measures should be established for each river, *ii*) experiments with breeding and releasing of smolt should continue, and *iii*) a laboratory for these efforts should be constructed. In 1952 in such a laboratory was built in Hölle in the Province of Jämtland. In 1961 the Swedish Salmon Research Institute (LFI) was established in Älvkarleby just south of Gävle. This institute was financed by hydro power companies (Lindroth 1984).

The work and suggestions from the investigation group formed the basis for how river plans and compensatory releases and water court rulings on such releases were performed. The steps were as follows:

1. Hydro power companies apply to the Environmental court suggesting amount of annual compensatory releases that they can perform in a particular river.
2. The Environmental Court consults with the Swedish Board of Fisheries (Fiskeriverket) and the State Attorney office (Kammarkollegiet).
3. The Environmental Court takes a preliminary decision on amount of smolt to be released, followed by a permanent decision.
4. The County Administrative Boards are the bodies that are to control the performance of the rulings.
5. The Swedish Salmon Research Institute provided advice to both the Swedish Board of Fisheries and to the hydro power companies on releases (Lindroth 1984).

The question on the extent of smolt releases has caused large problems in the court process where agreements must be reached between the hydro power companies and by the fish experts employed by the Environmental courts. The idea is to compensate for lost natural reproduction and to release smolt in the same magnitude as would have been produced naturally. Methods to get information on the natural smolt production have been through *i)* quantification of natural smolt production by trapping smolt (e.g. in the River

Rickleån 1963-1969), *ii)* surveying parr densities and year class distributions, *iii)* through mark and recapture of wild and reared smolt in natural rivers, *iv)* comparing catch statistics from neighbor rivers over extended long time series, and *v)* through tagging and recapturing fish from specific population (Lindroth 1984).

Swedish Water Court decisions follow the "äldre vattenlagen" SFS 1918:523 to 1993, the "nya vattenlagen" 193:291 to 1998, and since 1999 the Swedish Environmental Code 1998:808. Today, hydropower production is high in Sweden; in 2009, almost half (48.8%) of the total net electricity production in Sweden was produced by the current 1900 hydropower plants (SEA 2010). About 50 of these plants have a capacity of 100MWh or more (SEA 2010), and most of these large stations were built in the mid 20th century (www.vattenfall.se).

Rulings regarding compensatory releases stem from awide period of time, from 1960s to 2006. Only a few of the enhancement obligations are final judgments (for the Rivers Luleälven, Indalsälven, and Ångermanälven) while the majority are temporary decisions and still under investigation (Karl-Erik Nilsson, County Administrative Board of Norrbotten and Hans Olofsson, County Administrative Board of Västernorrland, pers. comm.).

6.3 Hydropower plants and compensatory releases in Swedish Baltic salmon rivers

There are around 1900 hydropower plants in Swedish rivers, and the majority of them are located in 29 rivers flowing into the Baltic Sea that have or used to have natural salmon populations (Figure 2). Compensatory releases are today carried out in eight of these rivers (Figure 2; Appendix), of which six of them have no wild salmon and are totally dependent on hatchery reared individuals to not lose their status as a salmon river. Court decision years and rulings for compensatory releases in individual rivers are presented in Appendix.

In most rivers exploited for hydropower purposes, there are no (or poor) possibilities for fish to migrate up the power plant dam to find spawning grounds. In some rivers, constructed fish ladders enable migration some tens of kilometers up the river.

For 22 of the Swedish salmon rivers flowing into the Baltic there are some legal protection from further water power plant developments (for the entire river or parts of the main river and/or tributaries) according to the Swedish Environmental Code (ch. 4, §6; see Appendix). Of those 22 rivers, four - Rivers Kalixälven, Piteälven, Torneälven, and Vindelälven - are classified as rivers of national importance (*In Swedish: nationalälv*).

Most hydropower companies have their own aquaculture facilities for producing fish for release, and compensatory releases are estimated to a cost of 80-100 million SEK per year (Swedish Agency for Marine and Water Management 2011).

6.3.1 Populations used for compensatory releases

A total of 30 salmon strains are used for large scale compensatory releases and stocking authorized by county administrative boards (Laikre et al. 2008, their Table 6). Regarding stocks used for compensatory releases, such information is available in an easily accessible way only for years 1999-2010. Court decisions do not specify the origin of releases in most cases, but the hydropower companies have adopted a policy of using local strains. However, in some cases non-local strains are used (e.g. Skellefte-strain is used in the River Gideälven) and in some cases the strain is unknown (database from Jens Persson, SLU). Also, some water court decisions allow salmon to be replaced by sea trout, or vice versa (e.g. in the River Indalsälven).

6.3.2 Amount of compensatory released salmon

The number of salmon obliged to be released are to be found in court decisions for individual rivers. According to these court decisions, in total c. 1.7 million salmon should be released annually in Swedish rivers flowing into the Baltic. However, these obligations can during individual years differ substantially from what is actually released. During the time period 1992-2010 (data from LFI yearbooks), c. 47 million hatchery reared individuals (of which c. 34 million have been smolt) have been released in Swedish Baltic rivers (Figure 3a-i), which make an annual average of c. 2.5 million individuals (of which c. 1.8 million are smolt). Of the total amount of salmon individuals released during these 19 years, c. 13 millions have been fin-clipped (the regulation regarding fin-clipping of all released fish in Sweden came into force in 2003/2004) and c. 270 000 have been Carlin tagged.

The total number of released individuals includes smolt, fry, and eggs. However, many court decisions specify that smoltificated individuals should be used for compensatory releases. Releases of fry and eggs may be the result of over production in hatcheries, experimental activities (concerning marking of individuals), and/or releases of fry and eggs as a replacement of smolt. Such releases should thus in some cases be seen as a part of the compensatory releases (Jens Persson, SLU, pers. comm.) but within the scope of this project it has been impossible to distinguish between situations when they should be seen as part of compensatory releases and when they should not.

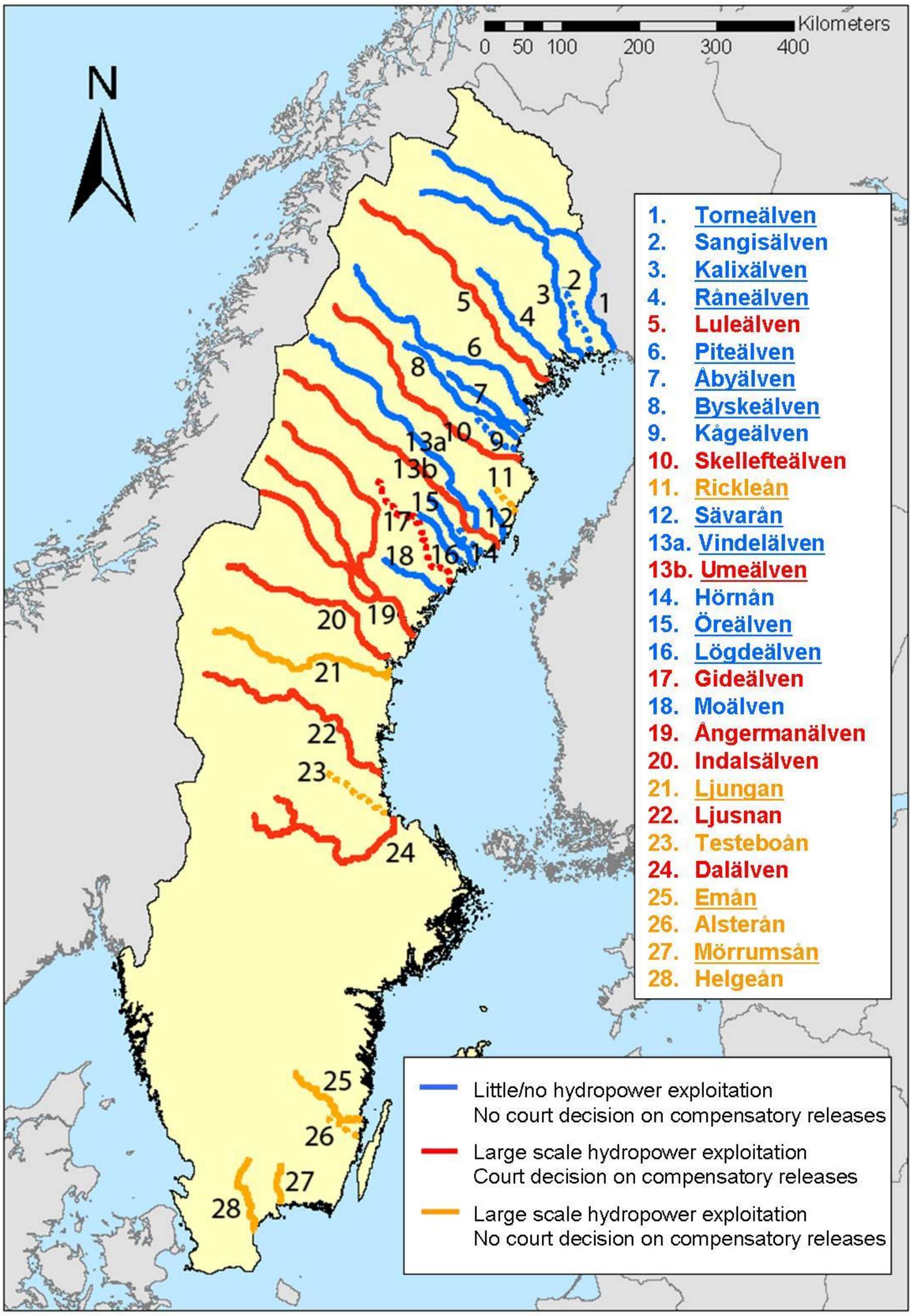


Figure 2. Swedish salmon rivers. Hydropower exploitation and compensatory release status for rivers are shown as blue, red, and yellow. Rivers marked with dashed lines are those without protection according to the Swedish Environmental Code, and rivers with wild salmon populations, as classified by the European Commission, are underlined in the figure legend. Note that Finnish compensatory releases are conducted in the River Torneälven.

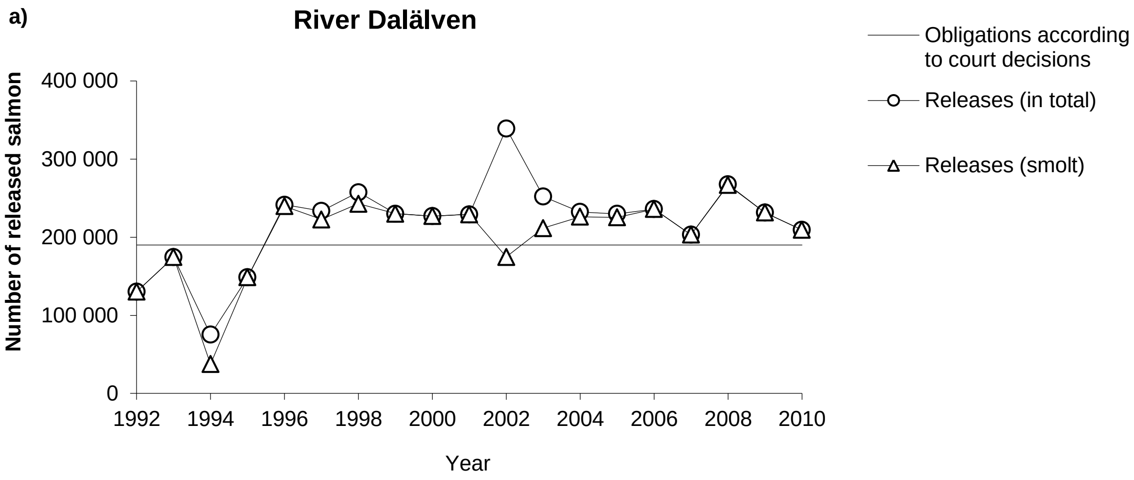
6.3.3 Procedures for producing smolt for releases

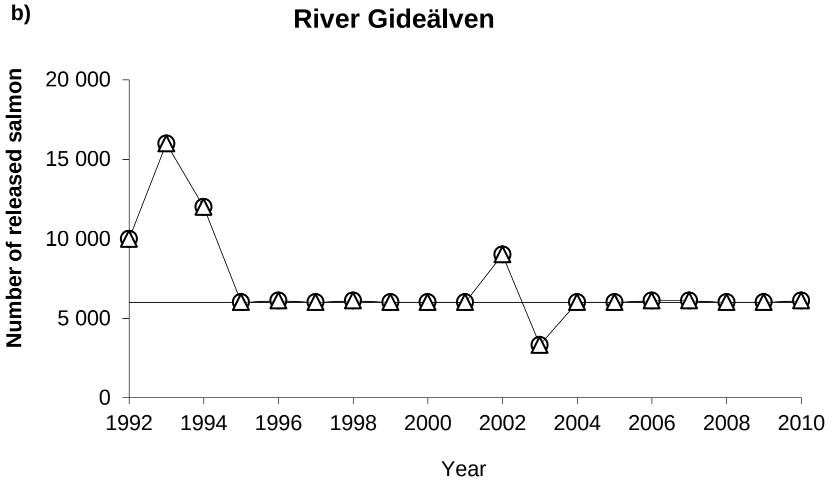
Swedish compensatory releases of salmon are exclusively based on individuals produced through sea ranching. This implies that spawners are collected from the wild each year and offspring is produced through collection of eggs and sperm. The offspring is released as smolt (at one or two years of age). Released fish are marked (fin-clipped) so that spawners produced in hatcheries can be separated from those resulting from possible natural reproduction. When spawners are collected, hatcheries have their own policies of mixing wild and hatchery produced males and females, dependent on the possibility for wild reproduction in that particular river.

Exactly how breeding at individual hatcheries is carried out is difficult to follow in detail. During the 1970-1980s it was noted that few parents were often used, resulting in inbreeding and inbreeding effects (Ståhl & Ryman 1987). Similarly, recommendations of mixing parent fish from different rivers were put forward (Rasmuson 1968). These problems do not appear to exist today. However, as far as we have been able to find out, the production of salmon smolt in hatcheries is not fully based on knowledge on possible within-river structure. For example, when collecting females and males to be used for rearing, the intention appears to be to maximize the genetic variation among spawners and fish are therefore collected during the entire returning to the river-period (i.e. spawners will represent both early and late migrating fish).

However, as far as we know, the fertilization is carried out without separating these groups of returning fish which implies that a potential genetic difference between early and late migrating fish is lost. Similarly, hatchery reproduction can never mimic natural conditions as mate choice and potential sexual selection is not possible.

Figure 3


a)
River Dalälven
Obligations according to court decisions
Releases (in total)
Releases (smolt)
Number of released salmon
400 000
300 000
200 000
100 000
0
1992
1994
1996
1998
2000
2002
2004
2006
2008
2010
Year


b)
River Gideälven
Number of released salmon
20 000
15 000
10 000
5 000
0
1992
1994
1996
1998
2000
2002
2004
2006
2008
2010
Year

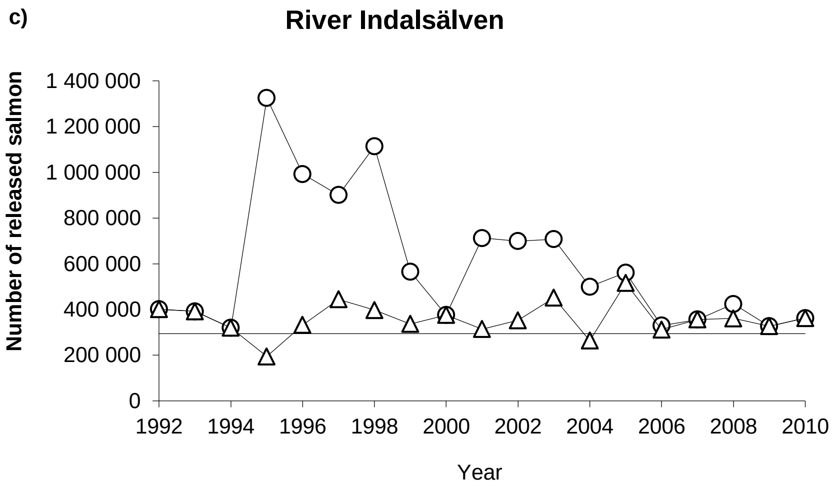
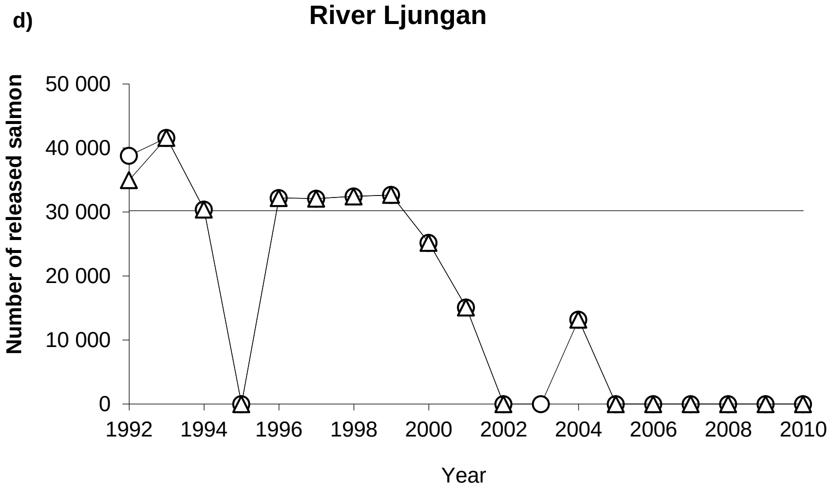
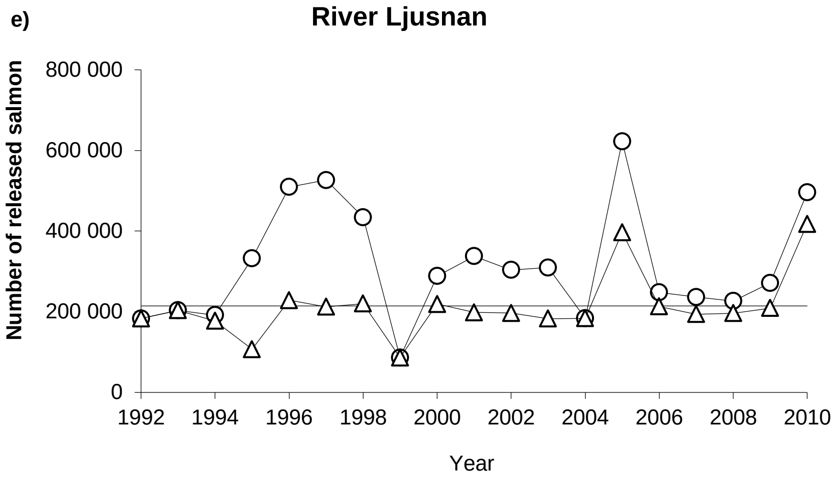

c)
River Indalsälven
Number of released salmon
1 400 000
1 200 000
1 000 000
800 000
600 000
400 000
200 000
0
1992
1994
1996
1998
2000
2002
2004
2006
2008
2010
Year

Figure 3


d)
River Ljungan
Number of released salmon
50 000
40 000
30 000
20 000
10 000
0
1992
1994
1996
1998
2000
2002
2004
2006
2008
2010
Year


e)
River Ljusnan
Number of released salmon
800 000
600 000
400 000
200 000
0
1992
1994
1996
1998
2000
2002
2004
2006
2008
2010
Year

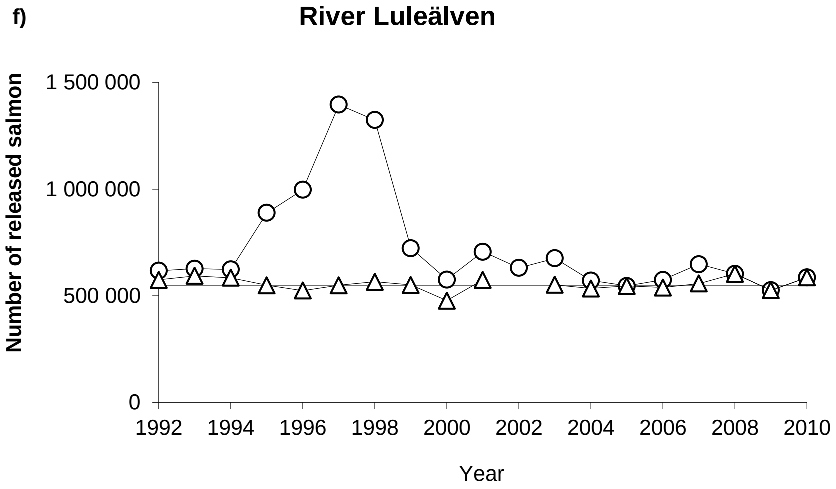
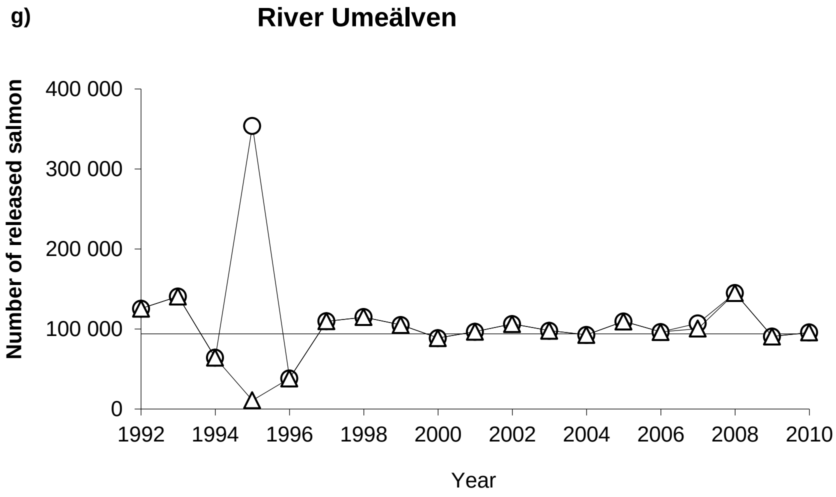
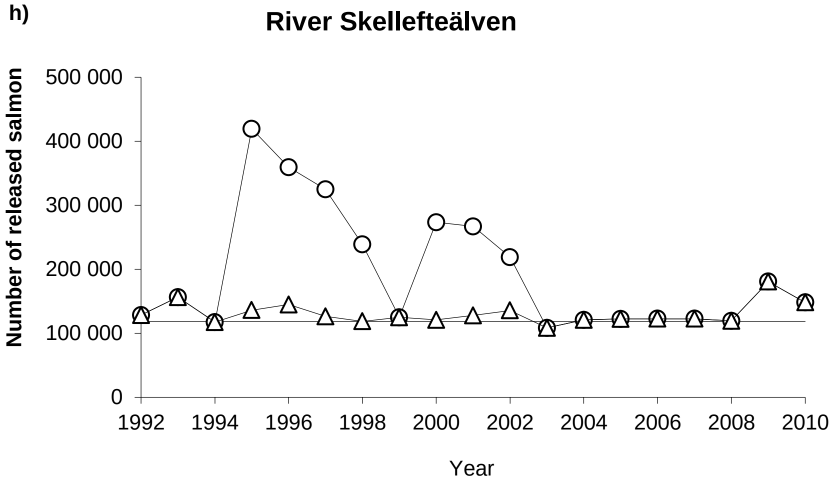

f)
River Luleälven
Number of released salmon
1 500 000
1 000 000
500 000
0
1992
1994
1996
1998
2000
2002
2004
2006
2008
2010
Year

Figure 3


g)
River Umeälven
Number of released salmon
400 000
300 000
200 000
100 000
0
1992
1994
1996
1998
2000
2002
2004
2006
2008
2010
Year


h)
River Skellefteälven
Number of released salmon
500 000
400 000
300 000
200 000
100 000
0
1992
1994
1996
1998
2000
2002
2004
2006
2008
2010
Year

i)

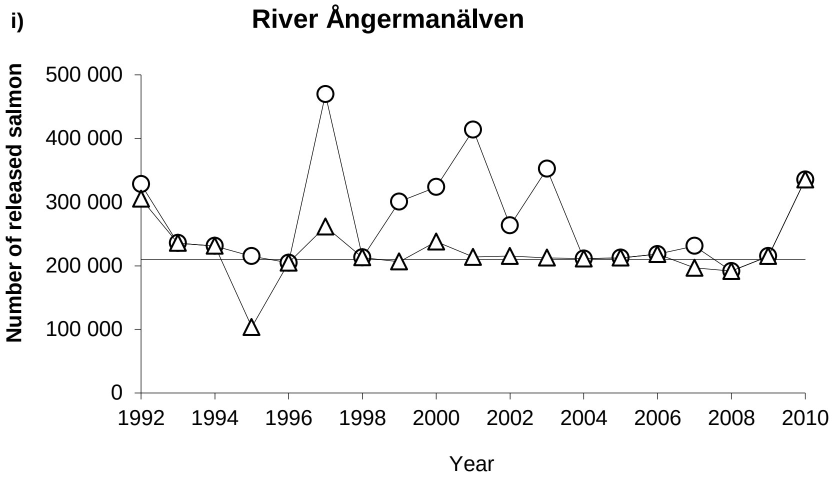


Figure 3. Number of salmon obliged to be releases according to court decisions and the actual number of released salmon during the period 1992-2010 (data from LFI yearbooks). The total number of released salmon (unfilled circles) includes releases of smolt, fry, and eggs. During the time period 1992-2010:

- *c.* 4.2 million salmon have in total been released in River Dalälven (plate a),
- *c.* 135 000 in River Gideälven (plate b),
- 11.4 million in River Indalsälven (plate c),
- 290 000 in River Ljungan (plate d),
- 6 million in River Ljusnan (plate e),
- 13.8 million in River Luleälven (plate f),
- 3.7 million in River Skellefteälven (plate g),
- 2.2 million in River Umeälven (plate h),
- and 5.2 million in River Ångermanälven (plate i).

Knowledge on both actual population size and the effective population size (N_e) are needed for effective conservation genetic management as these parameters strongly correlate to population viability (Luikart et al. 2010). While the actual population size affects the degree of demographic stochasticity, N_e determines the rate of loss of genetic variation. To avoid loss of genetic variation, a general rule-of-thumb regarding the effective population size is that N_e should not be less than 50 in the short term, and not fall below 500 in the long term. The effective population size is almost always considerable smaller than the actual population size, which means that a considerable large number of parents used in hatchery are needed to match the goal of long time genetic persistence.

It has been impossible to estimate N_e within the present project due to lack of appropriate data. However, for hatcheries producing smolt for compensatory release information is available on the number of males (N_m) and females (N_f) used in the breeding. We have used that data to estimate an "effective number of parents" (N_eP) per hatchery and year as

$$N_eP = \frac{4N_f N_m}{N_f + N_m}.$$

This equation (cf. Crow & Kimura 1970, p. 109) describes how the sex ratio affects the effective size, and for the present purpose N_eP can be interpreted as a first approximation of N_e.

Information on number of males and females used in rearing is only available for the time period 1965-2000. After the closure of LFI in 2001, this information seems not to be compiled by any authority.

During the period of 1965-2000, most of compensatory hatcheries never reached the goal of N_eP=500 (see Figure 4a-c). Only the hatchery at Heden (Lule-strain) exceeded this number during occasional years, while several hatcheries have figures of N_eP below 50 at repeated years (Figure 4a).

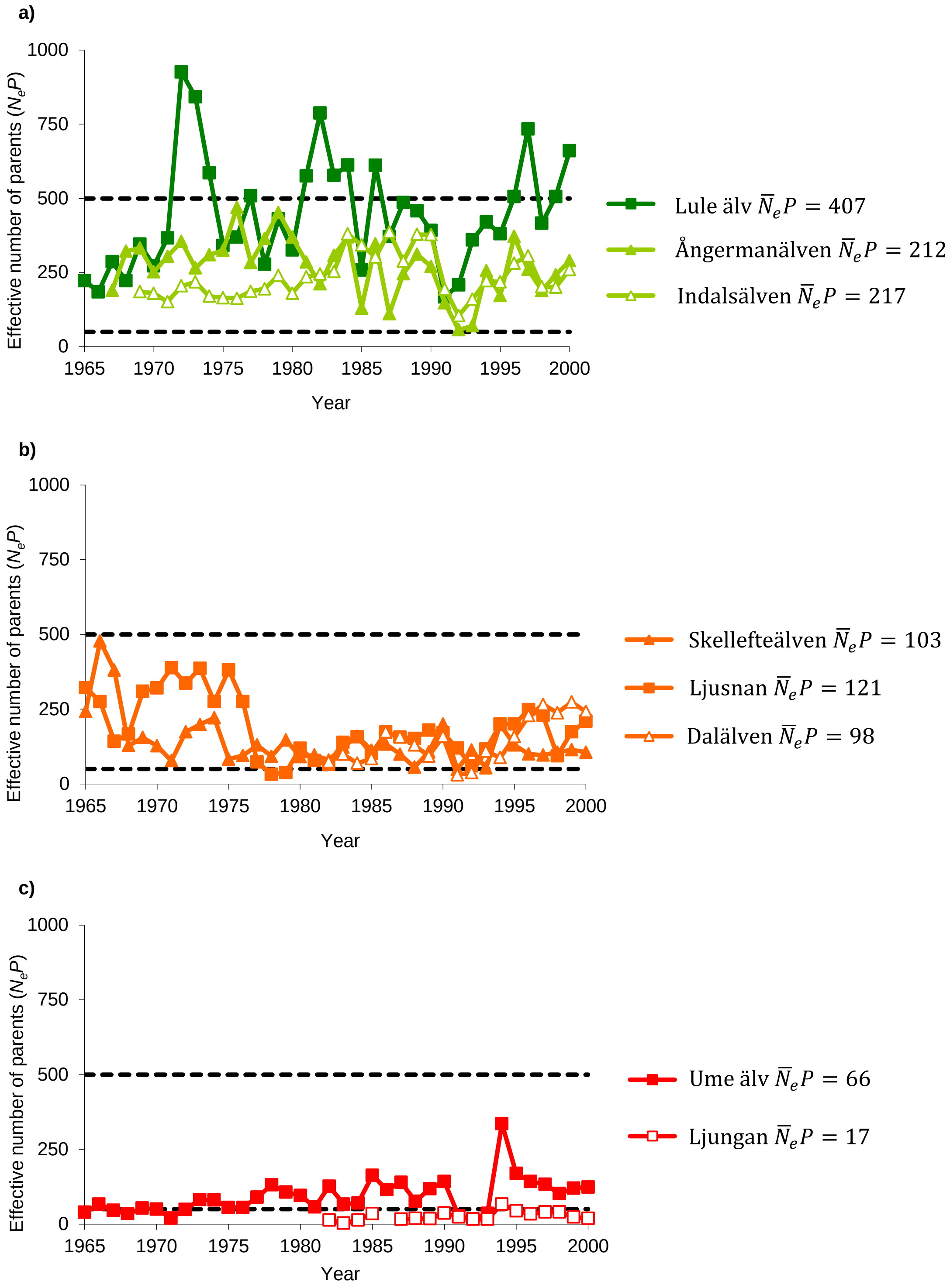


Figure 4. Effective number of parents (N_eP) for hatchery reared salmon stocks during the period 1970-2000. The calculations are based on the annual number of females and males used in each hatchery (data from Swedish Salmon Research Institute 2000). $\bar{N}_eP$ = harmonic mean for N_eP for the period 1970-2000. Dotted lines indicate N_e = 500 and N_e = 50, respectively. See text for details.

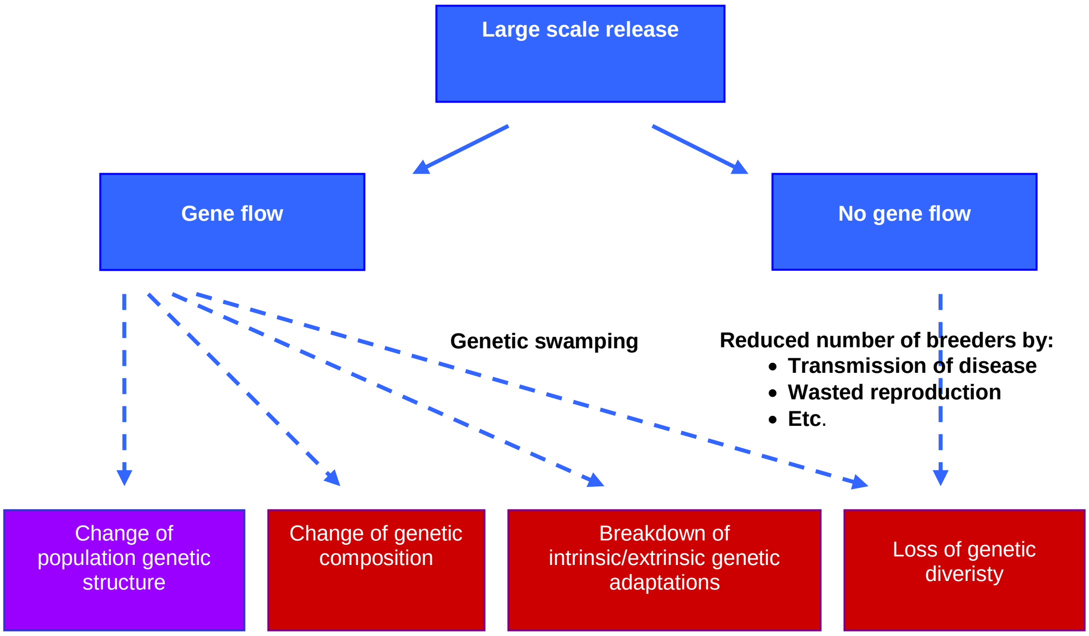
a) Salmon stocks with N_eP estimates never below 50.

b) Salmon stocks with more than one N_eP estimate below 50.

c) Salmon stocks with several N_eP estimates below 50.

7. Genetic risks of large scale releases

Releases of salmon are carried out to compensate for lost natural reproduction due to blocked migratory routes by hydroelectric power plants in rivers and to increase productivity of separate populations. Such releases may have demographic and economic, and probably in some cases also ecological incitements, but can cause four types of adverse impact on genetic biodiversity of remaining wild salmon populations: *1)* loss of genetic variation, *2)* loss of adaptations, *3)* change of population composition, and *4)* change of population structure (Laikre et al. 2010). These adverse genetic impacts have been recognized and documented for salmonid fishes for decades (Ryman 1981; Ryman & Utter 1987; Hindar et al. 1991; Waples 1999; Naish et al. 2008; Nielsen & Hansen 2008).



Modified from Laikre et al 2010 in Trends in Ecology and Evolution

Figure 5. Primary pathways by which large-scale releases can change genetic characteristics within (red boxes) and between (purple box) natural populations. From Laikre et al. 2010.

7.1 Empirical observations of genetic effects of releases in salmonid fishes

Genetic monitoring programs have documented each of the major effects illustrated in Figure 5 in salmonid fishes (Allendorf et al. 2001; Laikre et al. 2010). These effects refer both to between population diversity (Figure 5; purple box) and within population variation (red boxes).

7.1.1 Effects on between population genetic variation in salmonids

Change of population genetic structure: Massive releases of coho salmon (*Oncorhynchus kisutch*) have reduced the level of genetic differentiation between natural populations in Puget Sound, USA (Eldridge et al. 2007, 2009). Similarly, genetic structure was reduced between rivers that were stocked vs those that were not stocked in a study of Atlantic salmon population in 34 French rivers (Perrier et al. 2011).

In the Central Valley of California, extensive habitat modification and large hatchery programs with release strategies that promote widespread straying have genetically homogenized the metapopulation of fall-run Chinook salmon (*Oncorhynchus tshawytscha*; Lindley et al. 2009). After widespread recruitment failure in 2008, the U.S. imposed the most severe restrictions in history on west coast salmon fisheries. Lindley et al. (2009) concluded that a significant contributing factor to the collapse was related to a missing portfolio effect (Hilborn et al. 2003), i.e. loss of environmental buffering provided by a diverse array of natural populations.

A portfolio effect was also exemplified by population diversity effects of sockeye salmon (*Oncorhynchus nerka*) in Bristol Bay, Alaska. Long term data on population and life history diversity indicate that if the current several hundred discrete populations were replaced by a single population this would result in ten times more frequent fishery closures, ecosystem imbalance due to reduced predator and scavenger access to salmon resources, and a doubled inter annual variation with respect to the number of returning spawners (Schindler et al. 2010).

7.1.2 Effects on within population genetic variation in salmonids

Change of genetic composition: Mediterranean brown trout populations have suffered extensive introgression from genetically divergent hatchery stocks of Atlantic origin. Complete replacement of native gene pools with introduced ones occurs over large areas (García-Marín et al. 1999; Sanz et al. 2006; Araguas et al. 2009).

Similarly, the Adriatic grayling (*Oncorhunchus mykiss*), a morphologically and genetically distinct lineage in the north Adriatic basin, is endangered in the Soča River in Slovenia primarily due to several decades of extensive stocking with nonnative, genetically divergent stocks from the Danube. Introgression has caused the loss of 40-50% of the original gene pool, and pure indigenous grayling are difficult to find (Sušnik et al. 2004).

Breakdown of intrinsic and extrinsic genetic adaptations: Introgression of non-native genes has been reported to cause fitness reduction - outbreeding depression - in several salmonid species (Gharrett et al. 1999; Gilk et al. 2004; Tymchuk et al. 2007; Muhlfeld et al. 2009). Outbreeding depression can be caused by extrinsic and/or intrinsic factors (Allendorf et al. 2001). Releases can reduce fitness when alleles that contribute to local adaptation are replaced by ones that are locally non-adapted. This extrinsic type of fitness loss is frequently observed in the F1 generation (Tallmon et al. 2004).

Gene flow from a non-local source population can also cause breakup of co-adapted gene complexes, i.e. alleles at multiple loci that work synergistically to increase fitness (intrinsic adaptation). Because this breakup is caused by recombination, loss of adaptation generally occurs only in the F2 generation and beyond and can be much more difficult to detect than loss of extrinsic adaptation. Empirical examples from wild populations show that both types of adaptation can be lost by gene flow from genetically divergent populations (Gharrett et al. 1999).

Fitness effects can be insidious: in non-native rainbow trout (*Oncorhynchus mykiss*) that hybridized with native cutthroat trout (*Oncorhynchus clarkii lewisi*) in Montana, USA, the F1 offspring had high reproductive success. However, in subsequent generations fitness declined by nearly 50% (compared to fitness of native trout), following 20% introgression of non-native genes (Muhlfeld et al. 2009). Thus, increased F1 fitness due to heterosis can be misleading and followed by decreased fitness in F2 or later generations as co-adapted gene complexes are eroded.

A 37-year study of Atlantic salmon in Ireland found that naturally spawning farmed fish depress wild recruitment and disrupt the capacity of natural populations to adapt to higher water temperatures associated with climate change (McGinnity et al. 2009). Similarly, Hansen et al. (2009) examined Danish populations of brown trout subject to hatchery supplementation for 60 years and found evidence for selection in the wild against alleles associated with non-native hatchery fish.

Genetic changes in hatchery fish stocks due to domestication can result in severe effects on fitness of native populations they interact with. A two-generation experiment estimating lifetime success in the wild of wild native and farmed fish showed reduced survival in farmed Atlantic salmon and hybrids between wild and farmed fish. However, farmed fish and hybrids grew faster as juveniles and were able to displace wild parr (McGinnity et al. 2003). Similarly, reduction of reproductive success in the wild has been estimated to c. 40 percent per generation in a recent study of steelhead trout (*Oncorhynchus* spp.; Araki et al. 2007) Thus, even a few generations of domestication can have negative effects on natural reproduction in the wild.

7.1.3 Loss of genetic diversity without gene flow

Unintended introduction of the parasite *Gyrodactylus salaris* with Atlantic salmon from Sweden used in aquaculture caused the collapse of wild salmon populations in many Norwegian rivers (Peeler et al 2006). This classic case exemplifies loss of diversity not associated with gene flow from introduced populations.

7.1.4 Empirical observations from the Baltic

Surprisingly few studies of the genetic effects of large scale salmon releases in the Baltic Sea on native salmon gene pools exist. The early studies by Ståhl and coworkers showed that hatchery strains exhibited lower levels of genetic variation than the wild populations they were supposed to represent (Ståhl 1983), and that the genetic structure among hatchery populations differed from, and was less pronounced than, that among the wild populations (Ståhl 1987). These observations have been confirmed by later studies (e.g. Säisä 2003).

Also, indications of hybridization and inbreeding depression in hatcheries were reported from genetic studies of salmonid fish breeding programs at that time (Ståhl & Ryman 1987). These early results showing genetic changes and inbreeding in hatchery stocks and strong natural substructuring indicating low levels of natural genetic exchange between wild Baltic populations warranted monitoring the genetic effects of large scale stocking, but extremely few such studies have been carried out.

Vasemägi et al. (2005a) document genetic homogenization effects in the natural population of the River Vindelälven; the salmon of this river is becoming increasingly genetically similar to released hatchery stocks. Introgression rates from hatchery stocks into the native population are estimated as 5-25%, causing a trend of genetic homogenization over a decade (Vasemägi et al. 2005a). This is particularly serious as the wild population of River Vindelälven is one of only 15% remaining native, genetically distinct salmon populations in the Baltic.

7.1.5 Domestication of hatchery stocks

Selection in hatcheries resulting in domestication of hatchery stocks is a well know phenomenon in salmonid fishes (Fleming & Einum 1997; Kallio-Nyberg et al. 2007). The number of studies documenting such domestication effects, and the results of domestication in terms of changed physiology, and behavior followed by fitness effects is extensive (McGinnity 2003; Christie et al. 2011).

In Sweden the system with sea ranching results in a smaller likelihood of domestication, although such effects cannot be excluded. In Finland sea ranching is not practiced, instead brood stocks are used in hatcheries to produce fish for release. Domestication effects in Finnish salmon stocks have been shown to occur (Kallio-Nyberg & Koljonen 1997; Kallio-Nyberg et al. 2007).

7.2 Effects of supportive breeding

Supportive breeding refers to a means of supporting weak, wild stocks by bringing a fraction of the returning spawners into a hatchery and releasing their progeny into the river where they mix with wild conspecifics of the same stock (Ryman & Laikre 1991). The logic behind this type of capture-release program is to increase the number of smolt from the returning breeders without introducing non-local genes into the wild population. Although supportive breeding is clearly better than practices where exogenous genes are introduced into the wild population, this type of stocking may also have pronounced harmful effects by increasing the rate of inbreeding and loss of genetic variation. These effects result from the manipulation of reproductive rates caused by substantially more offspring being produced from the breeders brought into captivity than from those reproducing in the wild. Special care must be exercised when conducting supportive breeding such that the pros and cons of this approach are balanced and excessive loss of genetic variation is avoided (Ryman & Laikre 1991; Wang & Ryman 2001; NRC 2004).

8. Conservation genetic aspects associated with large scale salmon releases

Large scale releases are associated with a multitude of genetic risks for native populations, and such risks and effects are well documented for salmonid fishes (reviewed in Chapter 7). The current EU proposal of halting compensatory releases of salmon in the Baltic Sea is thus in line with our present best general knowledge regarding risks for native populations. However, our review also shows that the genetic effects of salmon releases in the Baltic are not well studied. In fact, genetic monitoring efforts aiming at evaluating the long term consequences of dam constructions and massive stocking operations on remaining wild salmon genetic biodiversity is almost completely missing (but see Vasemägi et al. 2005a).

Similary, an important issue concerns the extent to which genetic variation of Baltic salmon is maintained in hatchery stocks and through reproduction in hatcheries. For instance, Vasemägi and coworkers (2005b) analyzed wild and hatchery populations from the Gulf of Finland and the Gulf of Bothnia and found more genetic variation in hatchery stocks than in the wild populations from the Gulf of Finland.

The following questions are of key importance when assessing the effects on Baltic salmon gene pools from the past few decades of habitat alteration and release policies.

- What are the effects of releases on genetic variability between and within wild salmon populations?
- How has the loss of salmon populations affected the overall capacity for Baltic salmon to maintain genetic variation?
- How much of the overall genetic variability of Baltic salmon exists exclusively in hatcheries or is maintained exclusively through breeding-release operations?

As far as we have been able to find out, these issues have not yet been comprehensively addressed. It is beyond the scope of the current, limited review/synthesis to investigate these issues in depth, but we highlight some aspects of these questions below, in part through new analyses of some previously unpublished data.

8.1 Straying rates of released salmon

A key issue with respect to the genetic effects of the long term compensatory releases is the extent to which released salmon spread genes to other rivers than the one they are released into. There are few studies focusing on straying of salmon in the Baltic Sea, but a study by Vasemägi et al. (2005a) indicates that the “genetic pollution” from released salmon into wild populations can be as high as 5-25 percent.

We obtained recapture data from released hatchery reared salmon that were marked using Carlin tags during the period 1985-2010 from Jens Persson at the Swedish University of Agricultural Sciences (SLU), and the information is summarized in Table 4. These data have not been published previously, and it should be noted that there are ambiguities in the database that lead to uncertainties in the results presented in this table (Jens Persson, SLU, pers. comm.). Also, it is of course unclear if individuals recaptured in non-release rivers would actually have reproduced in the river where they were found if they had not been caught. Nevertheless, these observations seem to be consistent with the notion that gene flow from released, non-native stocks into wild populations can be substantial. The overall recapture rate in non-release rivers is 4 percent and the rates vary between 1 and 35 percent depending on hatchery stock (Table 4). There is no tendency for fish from single hatchery stocks to stray to particular rivers. For example, recaptured fish originating from, and released in, the River Dalälven are found in seven rivers (except from River Dalälven), which are located in a wide geographic range.

Table 4. Number of recaptured hatchery reared salmon with Carlin tags found in Swedish rivers, and the percent of strayed fish and river for recaptures of strayers, during 1985-2010. For example, 495 salmon with Carlin tags released in River Ångermanälven have been captured. Of these fish, 491 were caught in River Ångermanälven and four had strayed to other rivers (1 percent). Two of these were caught in River Ljusneforsen, one in River Umeälven, and one in another river but it is not clear in which one. Data obtained from Jens Persson, Swedish University of Agricultural Sciences.

Release river	**River number (according to Figure 1 and 2)**	**Number of marked recaptures**	**Number of fish recaptured in release river**	**Number of fish recaptured in non-release river**	**% straying**	**River for recapture of strayers (no. of individuals in parenthesis)**
Dalälven	24	252	238	14	6	Ljusneforsen (3) Ångermanälven (3) Skellefteälven (1) Byskeälven (1) Indalsälven (2) Ljusnan (2) Luleälven (2)
Gideälven (Skellefte-strain)	17	23	15	8	35	Ångermanälven (3) Skellefteälven (1) Dalälven (1) Unknown (3)
Indalsälven	20	274	270	4	1	Dalälven (1) Ångermanälven (2)
Ljungan	21	24	19	5	21	Indalsälven (3) Ångermanälven (1) Unknown (1)

Release river	**River number (according to Figure 1 and 2)**	**Number of marked recaptures**	**Number of fish recaptured in release river**	**Number of fish recaptured in non-release river**	**% straying**	**River for recapture of strayers (no. of individuals in parenthesis)**
Ljusnan	22	59	49	10	17	Ångermanälven (7) Dalälven (1) Unknown (2)
Luleälven	5	266	249	17	6	Piteälven (9) Umeälven (1) Skellefteälven (2) Ätran (1) Åbyälven (1) Unknown (3)
Piteälven	6	21	20	1	5	Skellefteälven (1)
Skellefteälven	10	120	119	1	1	Gideälven (1)
Umeälven/ Vindelälven	13ab	106	97	9	8	Ångermanälven (6) Ljusneforsen (1) Unknown (2)
Ångermanälven	19	495	491	4	1	Umeälven (1) Ljusneforsen (2) Unknown (1)
Total		**1 640**	**1 567**	**73**	**4**	

8.2 Genetic variation in wild vs. hatchery salmon populations

A potential negative effect of halting compensatory releases is that genetic variation maintained exclusively through hatchery breeding may be lost. Addressing the extent of this problem includes comparing the amount of genetic variation residing within and between hatchery stocks to that of wild populations.

8.2.1 Hierarchical gene diversity analyses

We illustrate one possible approach to the issue of the amount of genetic variation that occurs in wild vs. hatchery populations using allele frequency data for salmon on five allozyme loci provided by Dr. Gunnar Ståhl (previously at Stockholm University) and Dr. Håkan Jansson (previously at the Swedish Salmon Research Institute, LFI). This material was collected 1980-1999, and only some parts of the data have been published before. The reason for using this old material is that it represents rivers from which data from both hatchery and wild populations exist, and from which multiple samples separated in space and/or time are available from each wild population/hatchery stock. As shown in Tables 3a and 3b this kind of data is relatively rare (five rivers reported in the scientific literature and three in the “gray” literature). The material used here represents the Swedish Rivers Byskeälven, Dalälven, Emån, Ljungan, Muonioälven, Torneälven, and Umeälven.

We performed hierarchical gene diversity analyses using the program NEGST (Chakraborty et al. 1982), first considering the following sources of variation: “river”, “hatchery versus wild within rivers” and “between samples within river or stock”. We find that the between river component is the most important source of variation – with almost 60 percent (58%) of the “explained” variation being due to genetic differences between these seven rivers (Figure 6a; here “explained” variation implies variation that can be explained by the given hierarchical levels (11%), and unexplained variation represents variation within the bottom level of the hierarchy (89%). In this first case unexplained variation refers to variation within samples within river/hatchery stocks). Nearly one third – 28 percent – of the explained variation is due to differences between hatchery and wild populations within rivers, and 14 percent is explained by differences between samples from the same river obtained at different locations or different points in time (i.e. temporal variation; Figure 6a). In the next step we changed the hierarchical order (Figure 6b) and "hatchery vs. wild" then accounts for c. 6% of the explained variation, whereas "river" and "within-river" account for c. 80% and c. 14%, respectively.

Finally, we used the wild samples only (Figure 6c) and found that that ”river” represents the far most important source of variation when considering the levels “river” and “within-river” (i.e. spatial or temporal variation). “River” accounts for c. 93% of the “explained” variation, whereas “within-river” accounts for only c. 7% of the explained variation. Using a similar approach for hatchery stocks only (Figure 6d) ”river” and ”within-river” account for c. 77% and c. 23%, respectively.

Above hierarchical gene diversity analyses of seven hatchery stocks and the wild populations they are meant to represent indicate that *i*) there are clear genetic differences between wild populations and hatchery stocks of the same river, and *ii*) divergence is more pronounced among wild populations than among hatchery stocks. Thus, it appears that the hatchery populations may have contained a considerable portion of the gene pools of these rivers in the 1980s-1990s, and that the hatchery releases resulted in a reduction of genetic differences between wild populations (cf. Ståhl 1983; Vasemägi 2005b).

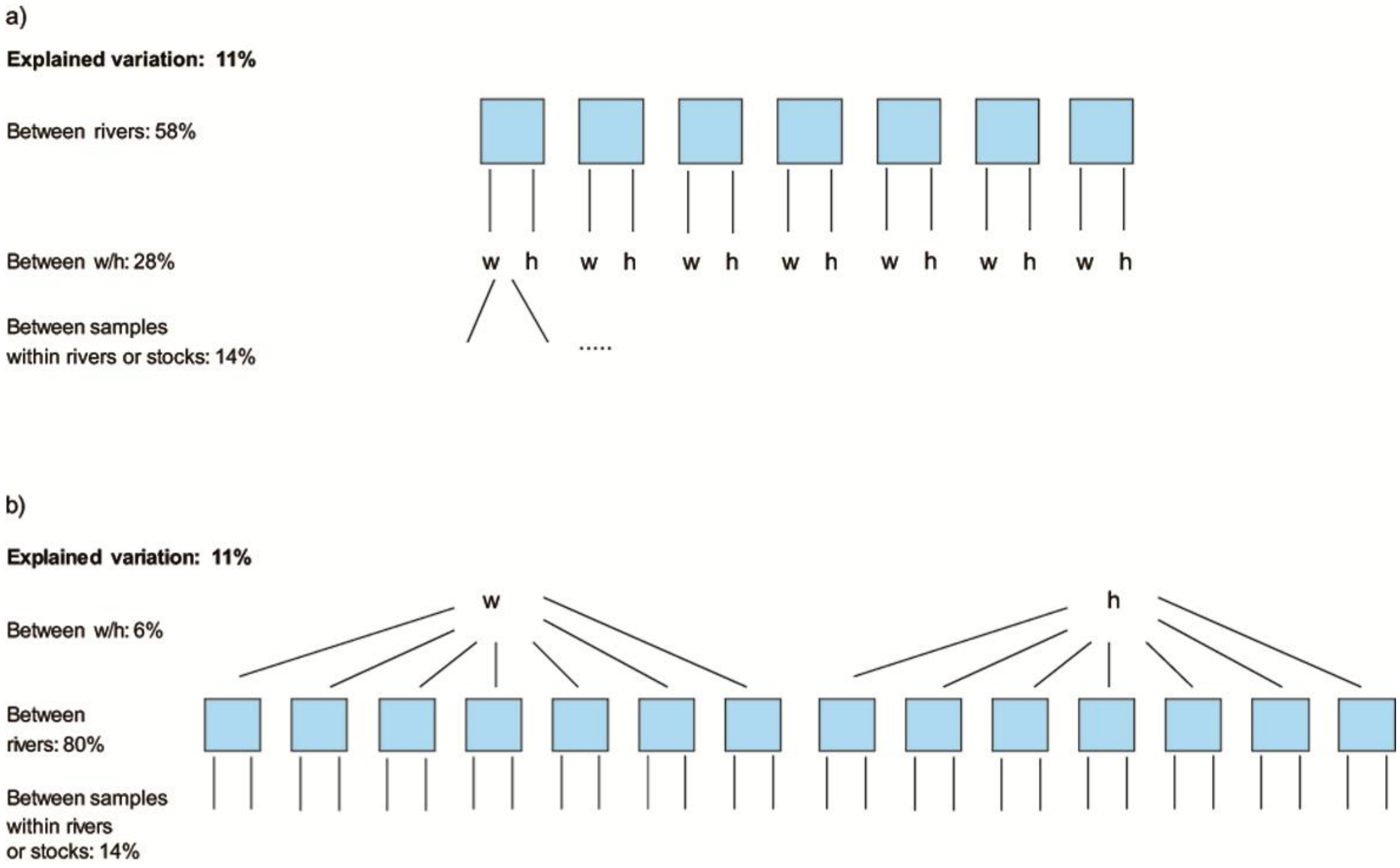


Figure 6

a)
Explained variation: 11%
Between rivers: 58%
Between w/h: 28%
Between samples within rivers or stocks: 14%
w h w h w h w h w h w h w h
.....
b)
Explained variation: 11%
Between w/h: 6%
w
h
Between rivers: 80%
Between samples within rivers or stocks: 14%

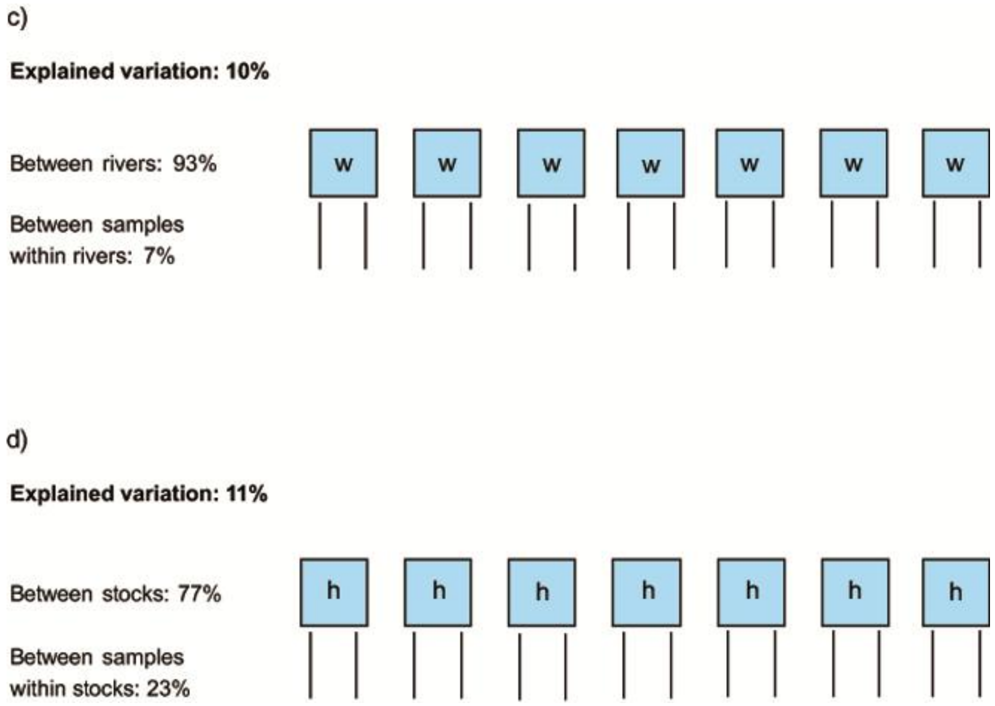


Figure 6. Results from hierarchical gene diversity analyses performed using the program negst (Chakraborty et al. 1982). The analyses are based on the variation at five allozyme loci in wild (w) and hatchery (h) samples from the following seven rivers: Byskeälven, Dalälven, Emån, Ljungan, Muonioälven, Torneälven, and Umeälven. a) The hierarchical order was: between rivers, between wild versus hatchery samples within rivers, and between within-river samples (i.e. spatial or temporal variation). b) The hierarchical order was: between wild versus hatchery samples, between rivers within each of wild and hatchery groups, and between within-river samples. c) Only wild samples were included and the hierarchical order used was between rivers and between within-river samples.
d) Only hatchery samples were included and the hierarchical order was between stocks and between within-stocks samples. See text for details.

8.2.2 Diversity and divergence patterns in hatchery vs. wild populations

Populations that are both genetically unique and have high internal genetic variation are expected to have a high probability of containing unique alleles and should be prioritized in conservation (Petit et al. 1998; Swatdipong et al. 2009).

We used allele frequency data from seven allozyme loci published in a study by Koljonen et al. (1999) to estimate relative genetic diversity and divergence from other populations for 14 wild Baltic salmon populations and 11 hatchery stocks (Figure 7). We used estimates of H_e as given in the article and further estimated pairwise divergence between populations as standard genetic distance using the software Dispan (Ota 1993). For each population relative internal diversity was calculated as the difference between H_e for the population in question and average H_e for all populations. Relative divergence for each population was calculated as the difference between the average genetic distance between the population in question and all other populations and the average genetic distance between all populations. Positive values for either diversity or divergence indicate that the population in question has higher internal diversity or is more diverged from other populations than average. Correspondingly, negative values indicate that the population in question has lower diversity or is less diverged from other populations than average.

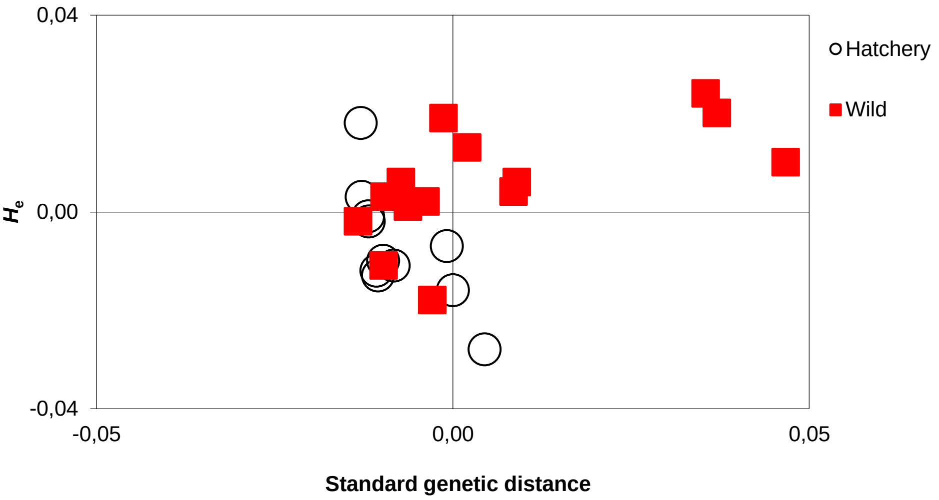


Figure 7. Relative divergence (Standard genetic distance) from other populations (on the X-axis) and relative diversity (H_e; on the Y-axis) for 14 wild Baltic populations and 11 Baltic hatchery stocks, based on data from Koljonen et al. (1999).

Further, we obtained genotypic data representing 17 microsatellite loci for 10 wild Swedish populations and seven Swedish hatchery stocks; in total 1 911 individuals (the data is a part of the ICES WGBAST baseline data generated between 1995-2006 in Dr. Marja-Liisa Koljonen´s laboratory). Average sample size (n) for wild samples is n=108 with a range of 25-167, and average sample size for hatchery samples is n=118 with a range of 113-120. We calculated H_e for each population and estimated pairwise divergence between populations as F_{ST}. To assess the relative diversity and divergence, the difference between H_e for the population in question and average H_e for all populations were calculated, as well as the difference between the average F_{ST} between the population in question and all other populations and the average pairwise F_{ST} between all populations. Estimates of relative genetic diversity and divergence are shown in Figure 8.

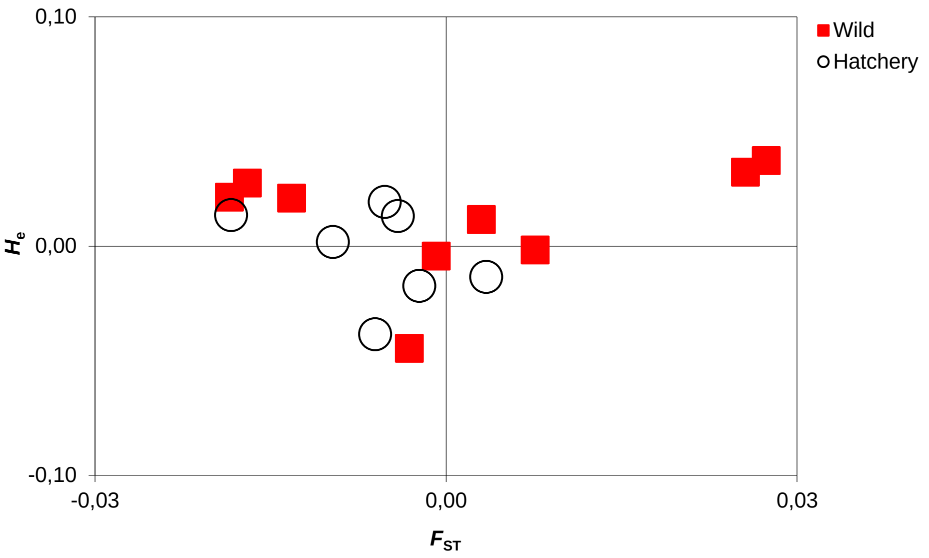


Figure 8. Relative divergence (F_{ST}) from other populations (on the X-axis) and relative diversity (H_e; on the Y-axis) for ten wild Swedish populations and seven Swedish hatchery stocks, based on data from Dr. Marja-Liisa Koljonen.

In both above analyses regarding diversity and divergence patterns, populations that are both more diverged from other populations than average and have high internal variation are exclusively of wild origin (Figures 7 and 8). These populations are both genetically unique and genetically "healthy" and should thus potentially be prioritized in conservation actions.

From the data representing Swedish wild populations and hatchery stocks (part of the ICES WGBAST baseline data), we also calculated the relationship between genetic and geographical distance (isolation by distance; IBD) between samples (Figure 9). The IBD was statistically tested with Mantel tests.

Figure 9 shows a highly significant IBD (correlation coefficient r=0.69, Mantel test P<0.001) for the wild salmon populations, but no similar pattern was found among the hatchery stocks (r=0.22, Mantel test P=0.29). The isolation by distance pattern for wild populations indicates that a stepping stone type of migration model is likely and that natural straying takes place mostly between nearby rivers. The lack of a significant IBD pattern for hatchery stocks can be explained by previous mixing of hatchery stocks.

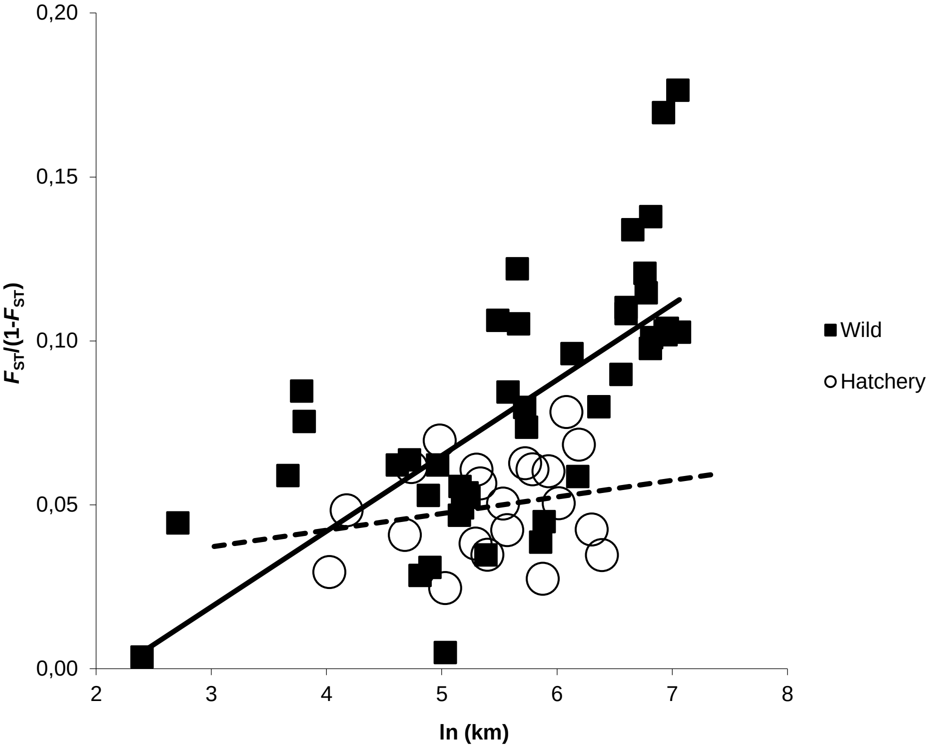


Figure 9. Pairwise relationship between genetic and geographical distance expressed as $F_{ST}/(1-F_{ST})$ and the natural logarithm of geographical distance for samples representing wild populations (black squares/solid line) and hatchery stocks (circles/dotted line). Data obtained from Dr. Marja-Liisa Koljonen. For wild populations the correlation coefficient (*r*) is 0.69 (Mantel $P<0.001$) and for hatchery stocks $r=0.22$ (Mantel $P=0.29$).

8.3 Effects on total genetic effective population size from population extinctions

One way of addressing the key question of the effects on genetic variation from losing a large proportion of the previous Baltic salmon populations is through assessing the expected reduction of the genetically effective population size (N_e) of the Baltic salmon population system as a whole (global effective size). This parameter is of key importance in conservation because it determines the rate of inbreeding and genetic drift, and thus the rate of loss of biodiversity at the gene level.

In a system of populations that are connected through migration there is a total (global) effective population size of the system as a whole, as well as local effective sizes of separate subpopulations which refer to the local N_e when the subpopulations are completely isolated.

We estimated the effect on global effective size when reducing the total number of salmon populations using analytical approaches of Hössjer and Ryman (submitted) and Wang and Caballero (1999) assuming an island model of migration and a linear stepping stone model, respectively. The most appropriate migration model for the Baltic salmon is not known, and we chose the island and the linear stepping stone models because they represent extremes with respect to global effective size for the same number of local populations, local effective sizes, and migration rates. We assumed a total number of 84 salmon populations (the number of Baltic rivers historically harboring wild salmon), and modeled the overall variance effective population size assuming local effective population sizes of 50-1000 and migration rates between 0.01-0.25. We evaluated the effect on overall (global) N_e of reducing the number of remaining populations to 27 (the number of remaining wild salmon rivers according to the European Commission) and to 10 (the number of safe wild salmon rivers according to CCB), respectively. We also made the simplified assumption that effective and census population size are equal.

The results show that at low migration rates overall (global) N_e can be much larger than the sum of the local N_es, and that this phenomenon is most pronounced for the linear stepping stone model (Table 5). This difference between the sum of local N_es and global N_e is most apparent with small local effective population sizes. For instance, with the stepping stone model, 84 subpopulations of effective size 50, and a migration rate of 0.01 the global N_e is almost ten times larger than the sum of local N_es (39 946 vs. 4 200; Table 5), whereas this difference is much smaller for the island model (6 265 vs. 4 200).

The results indicate that with an island model of migration the effect on global N_e of reducing the number of subpopulations is approximately equivalent to the proportion of remaining populations. That is, with 27 remaining populations overall N_e is reduced to 32 percent of what it is with 84 populations (27/84=0.32), and with 10 remaining populations overall N_e is reduced to 12 percent (10/84=0.12; Table 5). The results are more complicated with a stepping stone model and depend on both the local N_e and the migration rate. With lower local N_e and less migration the effects on overall N_e of reducing the number of subpopulations can be much more dramatic than indicated by the actual proportion of subpopulations lost. For example, with a migration rate of 1 percent (m=0.01) and local effective sizes of 50 the reduction from 84 rivers to 27 results in a 77 percent reduction of total N_e. Reducing the number of remaining rivers to 10 implies a reduction of 97.5 percent. At the same time, the global N_e is larger than for an island model with the same characteristics (Table 5).

Thus, evaluation of the effect of extinctions on the rate of loss of genetic variation requires information on migration rates and patterns as well as of effective sizes of the salmon populations of the separate rivers (and of multiple within river populations when appropriate). The isolation by distance (IBD) pattern reported in salmon (Koljonen et al. 1999; Säisä et al. 2005) suggests that a stepping stone type of migration model is more likely than the simplified island model.

These results stress the importance of conserving local populations in species with low migration rates and an isolation by distance patterns of migration. Clearly, the number of separate salmon populations maintained will have a large effect on the potential for retention of genetic variation over time. We expect that the dramatic loss of wild salmon populations in the Baltic have substantially reduced the total effective population size of the species in the Baltic resulting in elevated rates of loss of genetic variation.

Table 5. Effect on total (global) effective population size (Total N_e) of reducing the number of Baltic salmon river populations from 84 to 27 and 10, respectively. Two models of migration are used; the first segment refers to an island model and the second one to a stepping stone model. Local effective population sizes (N_e) vary between 50 and 1 000 and the migration rates (m) in the range 0.01-0.25.

Island model

84 remaining populations			**27 remaining populations**			**10 remaining populations**		
N_e	**m**	**Total N_e**	**N_e**	**m**	**Total N_e**	**N_e**	**m**	**Total N_e**
50	0.01	6 265	50	0.01	1 997	50	0.01	724
	0.05	4 604		0.05	1 477		0.05	544
	0.10	4 397		0.10	1 412		0.10	521
	0.25	4 271		0.25	1 372		0.25	508
100	0.01	10 465	100	0.01	3 347	100	0.01	1 224
	0.05	8 804		0.05	2 827		0.05	1 044
	0.10	8 597		0.10	2 762		0.10	1 021
	0.25	8 471		0.25	2 722		0.25	1 008
250	0.01	23 065	250	0.01	7 397	250	0.01	2 724
	0.05	21 404		0.05	6 877		0.05	2 544
	0.10	21 197		0.10	6 812		0.10	2 521
	0.25	21 071		0.25	6 772		0.25	2 508
500	0.01	44 065	500	0.01	14 147	500	0.01	5 224
	0.05	42 404		0.05	13 627		0.05	5 044
	0.10	42 197		0.10	13 562		0.10	5 021
	0.25	42 071		0.25	13 522		0.25	5 008
1 000	0.01	86 065	1 000	0.01	27 647	1 000	0.01	10 224
	0.05	84 404		0.05	27 127		0.05	10 044
	0.10	84 197		0.10	27 062		0.10	10 021
	0.25	84 071		0.25	27 022		0.25	10 008

Table 5 cont.

Linear stepping stone model								
84 remaining populations			**27 remaining populations**			**10 remaining populations**		
N_e	**m**	**Total N_e**	**N_e**	**m**	**Total N_e**	**N_e**	**m**	**Total N_e**
50	0.01	39 946	50	0.01	5 043	50	0.01	1 007
	0.05	11 349		0.05	2 089		0.05	601
	0.10	7 775		0.10	1 719		0.10	551
	0.25	5 630		0.25	1 498		0.25	520
100	0.01	44 146	100	0.01	6 393	100	0.01	1 507
	0.05	15 549		0.05	3 439		0.05	1 101
	0.10	11 975		0.10	3 069		0.10	1 051
	0.25	9 830		0.25	2 848		0.25	1 020
250	0.01	56 746	250	0.01	10 443	250	0.01	3 007
	0.05	28 149		0.05	7 489		0.05	2 601
	0.10	24 575		0.10	7 119		0.10	2 551
	0.25	22 430		0.25	6 898		0.25	2 520
500	0.01	77 746	500	0.01	17 193	500	0.01	5 507
	0.05	49 149		0.05	14 239		0.05	5 101
	0.10	45 575		0.10	13 869		0.10	5 051
	0.25	43 430		0.25	13 648		0.25	5 020
1 000	0.01	119 746	1 000	0.01	30 693	1 000	0.01	10 507
	0.05	91 149		0.05	27 739		0.05	10 101
	0.10	87 575		0.10	27 369		0.10	10 051
	0.25	85 430		0.25	27 148		0.25	10 020

8.4 Potentially unique genetic variation in hatchery stocks

To illustrate the genetic changes if compensatory releases are banned and the hatchery stocks are extirpated, we calculated total allele frequency divergence (F_{ST}), total expected heterozygosity (H_e), mean allelic richness, total number of alleles, and the number of private alleles for all 17 Swedish samples (including both hatchery stocks and wild populations) described above as well as for the ten wild samples only (Table 6). The results for the ten wild samples indicate the magnitude of change of these statistics if there would be only present-day wild Swedish populations. The most notable change is the loss of alleles if hatchery stocks are extirpated.

Table 6. Basic genetic statistics for the Swedish rivers in the data from ICES WGBAST baseline (2011) and for the Swedish wild populations. Data obtained from Dr. Marja-Liisa Koljonen. Allele frequency divergence (F_{ST}), expected heterozygosity (H_e), allelic richness, total number of alleles, number of private alleles, and the change (%) in these statistics if hatchery stocks are removed from the total dataset.

Statistics	**Wild populations and hatchery stocks**	**Only wild populations**	**% change**
F_{ST}	0.067	0.076	+13.7
H_e	0.713	0.715	+0.3
Allelic richness	7.76	7.81	+0.6
Total no. alleles	275	262	-4.7
No. of private alleles, i.e. alleles that only occur in one single population/stock	33	23	-30.3

8.5 Some reflections on genetic pros and cons of halting compensatory releases

As indicated from earlier work as well as from our above analyses there are several genetic risks associated with large scale releases of salmon. From a conservation genetic perspective our conclusion from previous and present work is that the most accurate action is to halt compensatory releases of salmon in the Baltic Sea. Such a halt is adequate provided that acceptable protection of wild populations is assured and that recovery plans for non self-sustainable populations are developed.

A key issue with respect to genetic effects of large scale releases is the rate of straying, i.e. genetic introgression from released fish into non-target wild populations. No clear-cut conclusion regarding typical introgression rates can be drawn from previous studies dealing with genetic effects of salmonid releases. Both high and low levels of introgression have been reported following long periods of repeated releases (low rates, e.g. Hansen et al. 2009; high rates, e.g. McGinnity et al. 2003; NRC 2002, 2004; Vasemägi et al. 2005a).

For the Baltic salmon there is a lack of information both on natural rates of migration between rivers and on actual straying rates from hatchery stocks into wild populations. These issues need to be further investigated to quantify the amount of introgression of hatchery genes into wild Baltic salmon populations. Our analyses indicate that one particular risk associated with salmon releases in the Baltic Sea is that several hatchery stocks do not genetically resemble the wild populations they were meant to represent, which may imply that they are not locally adapted to the environment they are released in. Further, Baltic salmon hatchery stocks seem to have lower genetic diversity within as well as between stocks compared to wild natural populations, and there is therefore an obvious risk of genetic homogenization of the total Baltic gene pool. Reduced genetic variability may lead to a decreased resilience to anthropogenic or natural disturbances. To better understand how large scale releases of hatchery reared salmon affect wild Baltic salmon populations, more in depth analyses are needed (see Chapter 9).

There seems to be few obvious genetic advantages of large scale salmon releases in the Baltic. It can be speculated that hatchery smolt may serve as a "predator shield" for wild smolt, leading to an increased survival of wild individuals and therefore a higher capacity for maintaining wild gene pools (John Piccolo, Karlstad University, pers. comm.). Further, some hatchery stocks appear to harbor unique alleles. Removing these stocks will result in a loss of genetic variation that is currently maintained exclusively through hatchery operations. Therefore, potential future use of hatchery stocks includes conservation stocking or keeping as gene banks.

Despite genetic risks associated with large scale enhancement actions, conservation releases can be justified to support or re-establish weak or extinct populations. Such measures must be evaluated on a case-by-case basis and the genetic effects of releases must be monitored.

9. Future research needs

The genetic risks associated with compensatory releases of salmon must be considered in conservation-management discussions, and relate to existing policy on conservation of biological diversity. Since the late 1970s considerable population genetics research has focused on salmonid species including the effects of stocking. Results from these efforts have warranted scientists to warn about the potentially negative effects of large scale releases on native gene pools (cf. Chapter 7; Laikre et al. 2010). Similarly, during recent years, efforts have been made to highlight the genetic situation of the Atlantic salmon in the Baltic Sea, exemplified by the present EU proposal of halting compensatory releases. However, both political and scientific measures are still needed with respect to regulating, documenting, and understanding the biological effects of large scale releases.

We do not think that further sampling currently represents the most urgent line of action, rather it appears that additional statistical evaluation of available genetic data, in combination with computer modeling can provide important information that is currently lacking in a cost-effective manner.

9.1 Documentation and archiving

Understanding genetic effects of compensatory releases on genetic variation between and within wild salmon populations relies on documentation of hatchery and release practices. Information on releases - from selection of spawners to releasing of fish - must be documented in a consistent, accessible, and straightforward manner. We suggest that steps are taken to investigate means and methods for uniform documentation and record keeping on hatchery breeding and release of salmon in the Baltic Sea area. Templates and effective computerized systems for such record keeping should be developed in collaboration with stakeholders including the Swedish Agency for Marine and Water Management and conservation genetic scientists. We suggest that a genetic advisory board is initiated to deal with this and other issues relating to the conservation of Baltic salmon gene pools. This board should include population and conservation geneticists from the Baltic countries.

Tissue sample archives provide a necessary basis for genetic monitoring. We suggest that the existence of such archives is reviewed to clarify the extent of stored tissues at various institutions in the Baltic countries. Such a review includes identifying institutions holding tissue or DNA samples from wild or hatchery populations of Baltic salmon, documenting the number of individuals, time and place of collection, and the extent to which genotypic data is available for these samples. Further, the possibility of creating a global database comprising the genotypes for the ~24 000 Baltic salmon that have been genotyped (cf. Table 3a and b) should be evaluated. Such a full dataset could be used for meta analyses of e.g. spatio-temporal variability patterns that, in turn, could be used for monitoring global and local gene pools.

9.2 Research

Although considerable genetic research has been devoted to Baltic salmon over the past few decades, several issues remain to be clarified that have not been possible to resolve within the scope of the present work. Such research may imply meta analyses using already existing information (compiled as suggested above) and/or collection of new data. Natural components of future research include:

- Computer modeling for in depth analysis of global and local effective population size of Baltic salmon as a basis for management decisions aimed at effective retention of remaining genetic variability.
- Estimates of effective (N_e) and actual population size of wild populations and hatchery stocks, their smolt production, relative survival, return rates, and contribution to fishery catches.
- Modeling and evaluating means to optimize global and local N_e using a meta population approach, including the expected effects of different harvesting and release regimes.
- Statistical assessment of the degree of genetic introgression that is possible to detect.
- Evaluation of sampling strategies for detecting different degrees of genetic introgression into wild populations from hatchery stocks.
- Assessment of the reduction in fishing pressure needed to maintain the genetic status of the Baltic salmon if compensatory releases are halted.
- Genetic monitoring of wild populations to study effects of large scale releases on naturally existing biological variation.
- Estimates of natural migration between rivers and straying rates of released individuals by assignment analysis using multi-locus genotypic data.
- Genetic characterization of wild salmon populations for which no genetic information exists today (10 wild salmon rivers lack genetic information out of the 27 ones identified by the European Commission).
- Assessment of remaining within-river variation due to e.g. early and late arriving spawners.
- Analysis of the degree of current genetic similarity between wild and hatchery stocks on a river-by-river basis.
- Assessment of the proportion of genetic variation that exists exclusively in hatcheries and of the amount of genetic variation that is expected to be lost by closing hatcheries.
- Development of strategies for conservation releases to support or re-establish weak/extinct wild salmon populations without threatening genetic biodiversity of non-target populations.
- Research on the potential positive effects of released hatchery smolt on wild smolt survival.

10. Conclusions and recommendations

We have evaluated the conservation genetic risks associated with compensatory releases of Atlantic salmon in the Baltic Sea. Our work has comprised *i*) reviewing all identified scientific studies of the genetics of Baltic salmon, *ii*) reviewing all identified “gray” literature on Baltic salmon genetics in Swedish rivers, *iii*) reviewing the scientific literature with respect to genetic effects of large scale releases of salmonid fishes, *iv*) compiling, with respect to the situation in Sweden, available material on the number of fish released annually, tagging data, and genetically effective number of parents, and *v*) conducting additional analyses based on published and unpublished genetic information.

Many aspects need to be considered in relation to the European Commission proposal to halt compensatory releases of salmon in the Baltic; they include ecological, socioeconomic, fisheries related issues, and the time frame for phasing out the compensatory releases. Our conclusions refer to the genetic aspects and can be summarized as follows:

1. The Atlantic salmon in the Baltic Sea is genetically irreplaceable in that it represents one of three major evolutionary units of the species. Each present salmon river harbors at least one genetically distinct population.
2. The extinction of a large number of wild populations has been harmful to the Baltic salmon; the capacity for retaining genetic variability has decreased as a consequence of a reduced genetically effective population size of the global population.
3. The global and the local effective population sizes have been further depleted through decreasing size of remaining local populations.
4. From a conservation genetics perspective the compiled information suggests that the proposal of the European Commission to halt compensatory releases of salmon in the Baltic is logical and sound.
5. Large scale releases constitute a potential threat to Baltic salmon genetic diversity. This is due to the genetic risks associated with *i*) gene flow from released hatchery stocks into wild populations, and *ii*) risks of overharvest of weak, wild populations because of increased numbers of salmon in the Baltic following the releases.
6. Little research has been devoted to empirically assessing the genetic effects of compensatory releases in the Baltic Sea, but observations from large scale salmonid releases in other geographical areas include: *i*) genetic homogenization of previously diverged populations, *ii*) complete or partial replacement of native gene pools, *iii*) break down of adaptations to local conditions, and *iv*) spread of diseases and parasites reducing absolute and effective sizes of native populations.

7. Comparisons of wild and hatchery stocks of the same river show that the genetic divergence between hatchery stocks is generally smaller than between wild ones. Further, there is a clear pattern of isolation-by-distance among wild populations, whereas no such pattern is found among hatchery stocks, suggesting that the natural genetic structure has not been maintained in hatcheries. This genetic homogenization might affect the capacity for local adaptation.
8. We have found only one monitoring study on genetic effects of compensatory releases in the Baltic Sea. In that study the scientists report a strong homogenizing effect on the genetic composition of the wild population in the River Vindelälven. This population became increasingly similar to hatchery stocks released in the neighboring area, and migration from hatchery stocks into the wild population was estimated as over 10 percent.
9. In most Swedish rivers the total number of released individuals, including smolt, fry, and eggs, exceeds the number of salmon obliged to be released according to court decisions. Crude estimates of effective population sizes (based on sex ratio only) show that Swedish salmon hatchery stocks frequently do not reach scientifically accepted levels for retaining genetic variation.
10. An unknown proportion of the current gene pool appears to be maintained exclusively through hatchery operations. Removing hatchery stocks will result in loss of genetic variation, but the extent of such loss remains unclear.
11. Strategies are urgently needed for maintenance of genetic variation that only exists in hatchery stocks, and for restoring as much as possible of the global Baltic salmon population through re-establishing spawning areas and opportunities for natural reproduction.

10.1 Recommendations

Based on our evaluation of the genetic risks associated with large scale compensatory releases of salmon in the Baltic we provide the following recommendations.

1. Compensatory releases of salmon in the Baltic should be phased out.
2. Releases in remaining salmon rivers that support wild, viable populations should be prohibited.
3. Conservation releases to support or re-establish weak/extinct populations can be used to protect and maintain as much as possible of the remaining Baltic salmon gene pool. The need for such releases should be evaluated on a case by case basis.
4. When releases are carried out they should always be monitored with respect to genetic effects, including those from supportive breeding because of the risk of reducing the genetically effective size of local populations.

5. The conservation genetic goal for Baltic salmon should be to create a global population that is as efficient as possible with respect to retaining genetic variation on a local and global scale.
6. A change of present fishing pressure is of key importance for the success of measures taken to improve the situation for, and the genetic status of, the Baltic salmon. It is critical that fishing pressures are modified in relation to changes in smolt production if compensatory releases are halted.
7. As many previous spawning areas and local populations as possible should be re-established.
8. The fate of individual hatchery stocks must be determined on a case by case basis. This can include *i*) using hatchery material for restoring or restocking rivers that presently do not support self sustaining populations, *ii*) keeping hatchery brood stocks or sea ranched populations as gene banks during a restricted period of time, and *iii*) prioritizing hatchery stocks with respect to their contribution to the global gene pool, and if necessary focus conservation actions on those stocks that contribute significantly. These operations must be coordinated and monitored, and may imply meta analysis using existing information and/or collection of new data for assessing the degree of current genetic similarity between wild and hatchery stocks.
9. A genetic advisory board should be initiated that includes population and conservation geneticists from all the Baltic countries. This board should supervise and coordinate national and international efforts to restore and maintain Baltic salmon gene pools as well as development of means and methods for consistent documentation and record keeping on hatchery breeding and release operations.
10. A review of existing archives of Baltic salmon tissue samples and genotypic data should be performed as soon as possible. Such resources provide an important basis for further genetic monitoring of Baltic salmon genetic biodiversity. Similarly, identifying the most critical gaps in currently available genotypic data constitutes a natural and important next step following the present synthesis report.
11. Several research issues remain to be addressed. Important cost effective work can be carried out without large scale additional genetic screenings building on already available genetic data.

11. Acknowledgments

Genetic data and other valuable information was kindly provided by **Marja-Liisa Koljonen** (Finnish Game and Fisheries Research Institute), **Gunnar Ståhl** (Biolab), **Håkan Jansson** (previously at the Swedish Salmon Research Institute, LFI), **Jens Persson** (Swedish University of Agricultural Sciences), and the **Coalition Clean Baltic**.

We thank the following persons for valuable input, discussions and suggestions: **Stefan Palm** (Swedish University of Agricultural Sciences), **Mats Grahn** (Södertörn University), **Ellen Bruno** (Swedish Society for Nature Conservation), **Johan Dannewitz** (Swedish University of Agricultural Sciences), **Peter Funegård** (Swedish Agency for Marine and Water Management), **Laura Piriz** (Swedish Agency for Marine and Water Management), **Gunnar Ståhl** (Biolab), **Johan Östergren** (Swedish University of Agricultural Sciences), **Michael M. Hansen** (Aarhus University), **Marja-Liisa Koljonen** (Finnish Game and Fisheries Research Institute), **Johan Tielman** (E.ON), **Jan Nilsson** (Swedish University of Agricultural Sciences), **Stefan Stridsman** (County Administrative Board of Norrbotten, previously at the Swedish Agency for Marine and Water Management), **Åke Forssén** (Vattenfall), **Ulf Carlsson** (County Administrative Board of Västerbotten), **Dan Blomkvist** (County Administrative Board of Norrbotten), **Karl-Erik Nilsson** (County Administrative Board of Norrbotten, previously at the Swedish Agency for Marine and Water Management), **Hans Olofsson** (County Administrative Board of Västernorrland, previously at the Swedish Agency for Marine and Water Management), **Jan Henricson** (previously at the former Swedish Board of Fisheries), **Gunnar Norén** (Coalition Clean Baltic), and **Nils Höglund** (Coalition Clean Baltic). We also thank an anonymous reviewer for valuable comments.

Funding was provided by The Swedish Agency for Marine and Water Management (LL), the BaltGene research program funded by BONUS Baltic Organisations' Network for Funding Science EEIG (LL & NR), and The Swedish Research Council Formas (LL & NR). The Sida Baltic Sea Unit and the Nordic Council of Ministers also supported the project.

12. References

Allendorf F, Ryman N, Stennek A, Ståhl G (1976) Genetic variation in Scandinavian brown trout (*Salmo trutta* L.) – evidence of distinct sympatric populations. Hereditas 83:73-82

Allendorf FW, England PR, Luikart G, Ritchie PA, Ryman N (2008) Genetic effects of harvest on wild animal populations. Trends in Ecology & Evolution 23:327-337

Allendorf FW, Leary RF, Spruell P, Wenburg JK (2001) The problems with hybrids: setting conservation guidelines. Trends in Ecology & Evolution 16:613-622

Allendorf FW, Luikart G (eds) (2007) Conservation and the Genetics of Populations. Blackwell Publishing, Malden

Allendorf FW, Phelps SR (1981) Isozymes and the preservation of genetic variation in salmonid fishes. Ecological Bulletins 34:37-52

Allendorf FW, Ryman N (1987) Genetic management of hatchery stocks. In: Ryman N, Utter F (eds) Population Genetics & Fishery Management. University of Washington Press, Seattle and London

Anderson EC, Waples RS, Kalinowski ST (2008) An improved method for predicting the accuracy of genetic stock identification. Canadian Journal of Fisheries and Aquatic Sciences 65:1475-1486

Araguas RM, Sanz N, Fernandez R, Utter FM, Pla C, Garcia-Marin JL (2009) Role of genetic refuges in the restoration of native gene pools of brown trout. Conservation Biology 23:871-878

Araki H, Cooper B, Blouin MS (2007) Genetic effects of captive breeding cause a rapid, cumulative fitness decline in the wild. Science 318:100-103

Beacham TD, Lapointe M, Candy JR, Miller KM, Withler RE (2004) DNA in action: Rapid application of DNA variation to sockeye salmon fisheries management. Conservation Genetics 5:411-416

Behnke RJ (1972) Systematics of salmonid fishes of recently glaciated lakes. Journal of the Fisheries Research Board of Canada 29:639-671

Bourke EA, Coughlan J, Jansson H, Galvin P, Cross TF (1997) Allozyme variation in populations of Atlantic salmon located throughout Europe: diversity that could be compromised by introductions of reared fish. ICES Journal of Marine Science 54:974-985

Chakraborty R, Haag M, Ryman N, Ståhl G (1982) Hierarchival gene diversity analysis and its application to brown trout population data. Hereditas 97:17-21

Child AR, Burnell AM, Wilkins NP (1976) Existence of two races of Atlantic salmon (*Salmo salar* L.) in British Isles. Journal of Fish Biology 8:35-43

Christie MR, Marine ML, French RA, Blouin MS (2012) Genetic adaptation to captivity can occur in a single generation. Proceedings of the National Academy of Sciences of the United States of America 109:238-242

CCB (Coalition Clean Baltic) (2012) Poster on the threats to the genetic diversity of the wild Baltic Salmon ¨Wild Baltic Salmon – the threat is real¨ (updated version). http://www.ccb.se/documents/Laxkarta_update2012.pdf)

Cross TF, Ward RD (1980) Protein variation and duplicate loci in the Atlantic salmon, *Salmo salar* L. Genetical Research 36:147-165

Crow JF, Kimura M (eds) (1970) An Introduction to Population Genetics Theory. Harper and Row, New York

Eldridge WH, Myers JM, Naish KA (2009) Long-term changes in the fine scale population structure of coho salmon populations (*Oncorhynchus kisutch*) subject to extensive supportive breeding. Heredity 103:299-309

Eldridge WH, Naish KA (2007) Long-term effects of translocation and release numbers on fine-scale population structure among coho salmon (*Oncorhynchus kisutch*). Molecular Ecology 16:2407-2421

European Commission (2011) Proposal for a Regulation of the European Parliament and of the Council establishing a multiannual plan for the Baltic salmon stock and the fisheries exploiting that stock. 470 final Brussels 12.8.2011. 2011/0206

Flannery BG, Beacham TD, Candy JR, Holder RR, Maschmann GF, Kretschmer EJ, Wenburg JK (2010) Mixed-Stock Analysis of Yukon River Chum Salmon: Application and Validation in a Complex Fishery. North American Journal of Fisheries Management 30:1324-1338

Fleming IA, Einum S (1997) Experimental tests of genetic divergence of farmed from wild Atlantic salmon due to domestication. ICES Journal of Marine Science 54:1051-1063

Fraser DJ, Weir LK, Bernatchez L, Hansen MM, Taylor EB (2011) Extent and scale of local adaptation in salmonid fishes: review and meta-analysis. Heredity 106:404-420

Gajardo G, Laikre L (2003) Chilean aquaculture boom is based on exotic salmon resources: a conservation paradox. Conservation Biology 17:1173-1174

Garcia-Marin JL, Utter FM, Pla C (1999) Postglacial colonization of brown trout in Europe based on distribution of allozyme variants. Heredity 82:46-56

Gharrett AJ, Smoker WW, Reisenbichler RR, Taylor SG (1999) Outbreeding depression in hybrids between odd- and even-broodyear pink salmon. Aquaculture 173:117-129

Gilk SE, Wang IA, Hoover CL, Smoker WW, Taylor SG, Gray AK, Gharrett AJ (2004) Outbreeding depression in hybrids between spatially separated pink salmon, *Oncorhynchus gorbuscha*, populations: marine survival, homing ability, and variability in family size. Environmental Biology of Fishes 69:287-297

Gärdenfors U (ed) (2010) The 2010 red list of Swedish species. Uppsala: The Swedish Species Information Centre Swedish University of Agriculture Sciences, ISBN 978-91-88506-35-1

Hansen LP, Jonsson N, Jonsson B (1993) Oceanic migration in homing Atlantic salmon. Animal Behaviour 45:927-941

Hansen MM, Fraser DJ, Meier K, Mensberg KLD (2009) Sixty years of anthropogenic pressure: a spatio-temporal genetic analysis of brown trout populations subject to stocking and population declines. Molecular Ecology 18:2549-2562

HELCOM (2007) HELCOM Red list of threatened and declining species of lampreys and fish of the Baltic Sea. Baltic Sea Environmental Proceedings, No. 109

HELCOM (2011) Salmon and Sea Trout Populations and Rivers in the Baltic Sea – HELCOM assessment of salmon (*Salmo salar*) and sea trout (*Salmo trutta*) populations and habitats in rivers flowing to the Baltic Sea. Baltic Sea Environmental Proceedings No. 126A

Hilborn R, Quinn TP, Schindler DE, Rogers DE (2003) Biocomplexity and fisheries sustainability. Proceedings of the National Academy of Sciences of the United States of America 100:6564-6568

Hindar K, Ryman N, Utter F (1991) Genetic effects of cultured fish on natural fish populations. Canadian Journal of Fisheries and Aquatic Sciences 48:945-957

Hössjer O, Ryman N (Submitted) Quasi equilibrium, variance effective size and fixation index for populations with substructure.

ICES (2003) Report of the Baltic Salmon and Trout Assessment Working Group (WGBAST). 2-11 April 2003, Karlskrona, Sweden. ICES CM 2003/ACFM:20

ICES (2009) Report of the Baltic Salmon and Trout Assessment Working Group (WGBAST). 24–31 March 2009, Oulu, Finland. ICES CM 2009/ACOM:05

ICES (2011) Report of the Baltic Salmon and Trout Assessment Working Group (WGBAST). 22–30 March 2011, Riga, Latvia. ICES2011/ACOM:08

Jackson JA, Laikre L, Baker CS, Kendall KC, The Genetic Monitoring Working Group (2012) Guidelines for collecting and maintaining archives for genetic monitoring. Conservation Genetic Resources 4:527-536

Jansson H (1993) A population genetic study of salmon from the Rivers Kalixälven and Torneälven. Swedish Salmon Research Institute, Älvkarleby, Report to the Swedish Board of Fisheries (in Swedish)

Jansson H (1995) Genetic follow-up of salmon and brown trout stocks reared for compensatory releases. Swedish Salmon Research Institute, Älvkarleby, Status report 1995-12-31 (in Swedish)

Jansson H (1997) Genetic follow-up of salmon and brown trout stocks reared for compensatory releases. Swedish Salmon Research Institute, Älvkarleby, Status report 1997-08-28 (in Swedish)

Jansson H, Öst T (1998) Genetic distinctness of salmon from the River Mörrumsån. Swedish Salmon Research Institute, Älvkarleby, Message 4/1998 (in Swedish)

Johannesson K, André C (2006) Life on the margin: genetic isolation and diversity loss in a peripheral marine ecosystem, the Baltic Sea. Molecular Ecology 15:2013-2029

Johannesson K, Smolarz K, Grahn M, André C (2011) The future of Baltic Sea populations: local extinction or evolutionary rescue? Ambio 40:179-190

Jones JW (1959) The Salmon. Collins, London

Kallio-Nyberg I, Saloniemi I, Koljonen ML (2007) Effects of parental and smolt traits on the marine survival of released Atlantic salmon (*Salmo salar*). Aquaculture 272:254-266

Kallio-Nyberg I, Koljonen ML (1997) The genetic consequence of hatchery-rearing on life-history traits of the Atlantic salmon (*Salmo salar* L.): a comparative analysis of sea-ranched salmon with wild and reared parents. Aquaculture 153:207-224

Klemetsen A, Amundsen PA, Dempson JB, Jonsson B, Jonsson N, O'Connell MF, Mortensen E (2003) Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* L.: a review of aspects of their life histories. Ecology of Freshwater Fish 12:1-59

Koljonen ML (1989) Electrophoretically detectable genetic variation in natural and hatchery stocks of Atlantic salmon in Finland. Hereditas 110:23-35

Koljonen ML (1995) Distinguishing between resident and migrating Atlantic salmon (*Salmo salar*) stocks by genetic stock composition analysis. Canadian Journal of Fisheries and Aquatic Sciences 52:665-674

Koljonen ML (2006) Annual changes in the proportions of wild and hatchery Atlantic salmon (*Salmo salar*) caught in the Baltic Sea. ICES Journal of Marine Science 63:1274-1285

Koljonen ML, Jansson H, Paaver T, Vasin O, Koskiniemi J (1999) Phylogeographic lineages and differentiation pattern of Atlantic salmon (*Salmo salar*) in the Baltic Sea with management implications. Canadian Journal of Fisheries and Aquatic Sciences 56:1766-1780

Koljonen ML, McKinnell S (1996) Assessing seasonal changes in stock composition of Atlantic salmon catches in the Baltic Sea with genetic stock identification. Journal of Fish Biology 49:998-1018

Koljonen ML, Pella JJ (1997) The advantage of using smolt age with allozymes for assessing wild stock contributions to Atlantic salmon catches in the Baltic Sea. ICES Journal of Marine Science 54:1015-1030

Koljonen ML, Pella JJ, Masuda M (2005) Classical individual assignments versus mixture modeling to estimate stock proportions in Atlantic salmon (*Salmo salar*) catches from DNA microsatellite data. Canadian Journal of Fisheries and Aquatic Sciences 62:2143-2158

Koljonen ML, Tahtinen J, Saisa M, Koskiniemi J (2002) Maintenance of genetic diversity of Atlantic salmon (*Salmo salar*) by captive breeding programmes and the geographic distribution of microsatellite variation. Aquaculture 212:69-92

Laikre L (ed) (1999) Conservation genetic management of brown trout (*Salmo trutta*) in Europe. Report by the concerted action on identification, management and exploration of genetic resources in the brown trout (*Salmo trutta*) ("TROUTCONCERT; EU FAIR CT97-3882)

Laikre L, Palm S, Ryman N (2005) Genetic population structure of fishes: Implications for coastal zone management. Ambio 34:111-119

Laikre L, Palmé A (2005) Release of alien populations in Sweden. Swedish Environmental Protection Agency, Report 5475 (in Swedish, English summary)

Laikre L, Palmé A, Josefsson M, Utter F, Ryman N (2006) Release of alien populations in Sweden. Ambio 35:255-261

Laikre L, Palmé A, Larsson LC, Charlier J, Ryman N (2008) Large scale releases of genetically alien populations in Sweden – An overview of the potentials for monitoring genetic effects on natural populations. Swedish Environmental Protection Agency, Report 5881 (in Swedish, English summary)

Laikre L, Schwartz MK, Waples RS, Ryman N, The Genetic Monitoring Working Group (2010) Compromising genetic diversity in the wild: unmonitored large-scale release of plants and animals. Trends in Ecology & Evolution 25:520-529

Langefors A, Lohm J, von Schantz T, Grahn M (2000) Screening of MHC variation in Atlantic salmon (*Salmo salar*): a comparison of restriction fragment length polymorphism (RFLP), denaturing gradient gel electrophoresis (DGGE) and sequencing. Molecular Ecology 9:215-219

Langefors A, Von Schantz T, Widegren B (1998) Allelic variation of MHC class II in Atlantic salmon; a population genetic analysis. Heredity 80:568-575

Langefors AH (2005) Adaptive and neutral genetic variation and colonization history of Atlantic salmon, *Salmo salar*. Environmental Biology of Fishes 74:297-308

Larsson PO, Larsson HO, Eriksson C (1979) Review of Swedish salmon (*Salmo salar* L.) stocks based on tagging experiments. Swedish Salmon Research Institute, Älvkarleby, Message 5 (in Swedish)

Lindley ST, Grimes CB, Mohr MS, Peterson W, Sein J, Anderson JT, Botsford LW, Bottom DL, Busack CA, Collier TK, Ferguson J, Gara JC, Grover AM, Hankin DG, Kope RG, Lawson PW, Low A, MacFarlane RB, Moore K, Palmer-Zwahlen M, Schwing FB, Smith J, Tracy C, Webb R, Wells BK, Williams TH (2009) What caused the Sacramento River fall Chinook stock collapse? NOAA Tech Memo NMFS-SWFSC 447

Lindroth A (1984) The Swedish salmon smolt releases in the Baltic Sea. Swedish State Power Board (present name of organisation is Vattenfall AB), Vällingby (in Swedish)

Lohm J (2002) Isolation-by-distance in river dwelling anadromous Atlantic salmon (*Salmo salar* L.). In: Lohm J (ed) MHC and genomic diversity in Atlantic salmon (*Salmo salar* L.). Doctoral thesis, Department of Ecology, Lund University

Luikart G, Ryman N, Tallmon DA, Schwartz MK, Allendorf FW (2010) Estimation of census and effective population sizes: the increasing usefulness of DNA-based approaches. Conservation Genetics 11:355-373

McCormick SD, Hansen LP, Quinn TP, Saunders RL (1998) Movement, migration, and smolting of Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 55:77-92

McGinnity P, Jennings E, DeEyto E, Allott N, Samuelsson P, Rogan G, Whelan K, Cross T (2009) Impact of naturally spawning captive-bred Atlantic salmon on wild populations: depressed recruitment and increased risk of climate-mediated extinction. Proceedings of the Royal Society B-Biological Sciences 276:3601-3610

McGinnity P, Prodohl P, Ferguson K, Hynes R, O'Maoileidigh N, Baker N, Cotter D, O'Hea B, Cooke D, Rogan G, Taggart J, Cross T (2003) Fitness reduction and potential extinction of wild populations of Atlantic salmon, *Salmo salar*, as a result of interactions with escaped farm salmon.

Proceedings of the Royal Society of London Series B-Biological Sciences 270:2443-2450

Møller D (1970) Transferrin polymorphism in Atlantic salmon (*Salmo salar*). Journal of the Fisheries Research Board of Canada 27:1617-1625

Muhlfeld CC, Kalinowski ST, McMahon TE, Taper ML, Painter S, Leary RF, Allendorf FW (2009) Hybridization rapidly reduces fitness of a native trout in the wild. Biology Letters 5:328-331

Naish KA, Taylor JE, Levin PS, Quinn TP, Winton JR, Huppert D, Hilborn R (2008) An evaluation of the effects of conservation and fishery enhancement hatcheries on wild populations of salmon. In: Sims DW (ed) Advances in Marine Biology, Book 53. Elsevier Academic Press Inc, San Diego

Nielsen EE, Hansen MM (2008) Waking the dead: the value of population genetic analyses of historical samples. Fish and Fisheries 9:450-461

Nilsson J (1997) MtDNA and microsatellite variation in Baltic Atlantic salmon. ICES Journal of Marine Science 54:1173-1176

Nilsson J, Gross R, Asplund T, Dove O, Jansson H, Kelloniemi J, Kohlmann K, Löytynoja A, Nielsen EE, Paaver T, Primmer CR, Titov S, Vasemägi A, Veselov A, Öst T, Lumme J (2001) Matrilinear phylogeography of Atlantic salmon (*Salmo salar* L.) in Europe and postglacial colonization of the Baltic Sea area. Molecular Ecology 10:89-102

Nilsson J, Östergren J, Lundqvist H, Carlsson U (2008) Genetic assessment of Atlantic salmon *Salmo salar* and sea trout *Salmo trutta* stocking in a Baltic Sea river. Journal of Fish Biology 73:1201-1215

NRC (National Research Council) (2002) Genetic status of Atlantic salmon in Maine. Interim Report. Washington, DC, National Academy Press

NRC (National Research Council) (2004) Atlantic salmon in Maine. Washington, DC, National Academy Press

Nyman OL, Pippy JHC (1972) Differences in Atlantic salmon, *Salmo salar*, from North-America and Europe. Journal of the Fisheries Research Board of Canada 29:179-185

OSPAR (2008) OSPAR convention for the protection of the marine environment of the North-East Atlantic: List of threatened and/or declining species and habitats. Reference number: 2008-06

OSPAR (2010) Background document for Atlantic salmon *Salmo salar*. OSPAR, London 480/2010

Ota T (1993) DISPAN: Genetic Distance and phylogenetic analysis. Pennsylvania State University, University Park, PA

Ozerov MY, Veselov AJ, Lumme J, Primmer CR (2010) Genetic structure of freshwater Atlantic salmon (*Salmo salar* L.*)* populations from the lakes Onega and Ladoga of northwest Russia and implications for conservation. Conservation Genetics 11:1711-1724

Palm S, Dannewitz J, Järvi T, Koljonen ML, Prestegaard T, Olsén KH (2008) No indications of Atlantic salmon (*Salmo salar*) shoaling with kin in the Baltic Sea. Canadian Journal of Fisheries and Aquatic Sciences 65:1738-1748

Palmé A, Wennerström L, Guban P, Laikre L (eds) (2012) Stopping compensatory releases of salmon in the Baltic Sea. Good or bad for Baltic salmon gene pools? Report from symposium and workshop, Stockholm University February 9-10 2012. Davidsons Tryckeri, Växjö, Sweden

Palmé A, Wennerström L, Guban P, Ryman N, Laikre L (2012) Conclusions on conservation genetic risks associated with compensatory releases of salmon in the Baltic Sea. A brief summary of a synthesis report to the Swedish Agency for Marine and Water Management. Department of Zoology, Division of Population Genetics, Stockholm University, Sweden.

Payne RH (1974) Transferrin variation in North-American populations of Atlantic salmon, *Salmo salar*. Journal of the Fisheries Research Board of Canada 31:1037-1041

Payne RH, Child AR, Forrest A (1971) Geographical variation in Atlantic salmon. Nature 231:250-252

Peeler E, Thrush M, Paisley L, Rodgers C (2006) An assessment of the risk of spreading the fish parasite *Gyrodactylus salaris* to uninfected territories in the European Union with the movement of live Atlantic salmon (*Salmo salar*) from coastal waters. Aquaculture 258:187-197

Pella JJ, Milner GB (1987) Use of genetic marks in stock composition analysis. In population genetics and fisheries management. In: Ryman N, Utter F (eds) Population Genetics & Fishery Management. University of Washington Press, Seattle and London

Perrier C, Guyomard R, Bagliniere JL, Evanno G (2011) Determinants of hierarchical genetic structure in Atlantic salmon populations: environmental factors vs. anthropogenic influences. Molecular Ecology 20:4231-4245

Petit RJ, El Mousadik A, Pons O (1998) Identifying populations for conservation on the basis of genetic markers. Conservation Biology 12:844-855

Rasmuson M (1968) Population genetic aspects of salmon rearing in Sweden. Swedish Salmon Research Institute, Älvkarleby, Message 3/1968 (in Swedish)

Rassi P, Hyvärinen E, Juslén A, Mannerkoski I (eds) (2010) The 2010 Red list of Finnish species. Ministry of the Environment and Finnish Environment Institute. Helsinki

Ryman N (1972) Analysis of growth capability in full sib families of salmon (*Salmo salar* L.). Hereditas 70:119-127

Ryman N (1981) Conservation of genetic resources – experiences from the brown trout (*Salmo trutta*). Ecological Bulletins 34:61-74

Ryman N (1983) Patterns of distribution of biochemical genetic variation in salmonids – differences between species. Aquaculture 33:1-21

Ryman N, Utter F (eds) (1987) Population genetics & fishery management. University of Washington Press, Seattle and London

Ryman N, Laikre L (1991) Effects of supportive breeding on the genetically effective population size. Conservation Biology 5:325-329

Ryman N, Ståhl G (1981) Genetic perspectives of the identification and conservation of Scandinavian stocks of fish. Canadian Journal of Fisheries and Aquatic Sciences 38:1562-1575

Ryynanen HJ, Primmer CR (2004) Distribution of genetic variation in the growth hormone 1 gene in Atlantic salmon (*Salmo salar*) populations from Europe and North America. Molecular Ecology 13:3857-3869

Ryynanen HJ, Tonteri A, Vasemägi A, Primmer CR (2007) A comparison of biallelic markers and microsatellites for the estimation of population and conservation genetic parameters in Atlantic salmon (*Salmo salar*). Journal of Heredity 98:692-704

Säisä M, Koljonen ML, Gross R, Nilsson J, Tahtinen J, Koskiniemi J, Vasemägi A (2005) Population genetic structure and postglacial colonization of Atlantic salmon (*Salmo salar*) in the Baltic Sea area based on microsatellite DNA variation. Canadian Journal of Fisheries and Aquatic Sciences 62:1887-1904

Säisä M, Koljonen ML, Tahtinen J (2003) Genetic changes in Atlantic salmon stocks since historical times and the effective population size of a long-term captive breeding programme. Conservation Genetics 4:613-627

Sanz N, Cortey M, Pla C, Garcia-Marin JL (2006) Hatchery introgression blurs ancient hybridization between brown trout (*Salmo trutta*) lineages as indicated by complementary allozymes and mtDNA markers. Biological Conservation 130:278-289

Schindler DE, Hilborn R, Chasco B, Boatright CP, Quinn TP, Rogers LA, Webster MS (2010) Population diversity and the portfolio effect in an exploited species. Nature 465:609-612

SEA (Swedish Energy Agency) (2010) Energy in Sweden – facts and figures 2010. Swedish Energy Agency

Shaklee JB, Beacham TD, Seeb L, White BA (1999) Managing fisheries using genetic data: case studies from four species of Pacific salmon. Fisheries Research 43:45-78

Stabell OB (1984) Homing and olfaction in salmonids – a critical review with special reference to the Atlantic salmon. Biological Reviews of the Cambridge Philosophical Society 59:333-388

Ståhl G (1981) Genetic differentiation among natural populations of Atlantic salmon (*Salmo salar*) in Northern Sweden. Ecological Bulletins 34:95-105

Ståhl G (1983) Differences in the Amount and distribution of genetic variation between natural populations and hatchery stocks of Atlantic salmon. Aquaculture 33:23-32

Ståhl G (1987) Genetic population structure of Atlantic salmon. In: Ryman N, Utter F (eds) Population Genetics & Fishery Management. University of Washington Press, Seattle and London

Ståhl G, Ryman N (1987) Salmon and brown trout in the Lake Vänern area – A population genetic analysis. Swedish Environmental Protection Agency, Report 3357 (in Swedish)

Sušnik S, Berrebi P, Dovĉ P, Hansen MM, Snoj A (2004) Genetic introgression between wild and stocked salmonids and the prospects for using molecular markers in population rehabilitation: the case of the Adriatic grayling (*Thymallus thymallus L.* 1785). Heredity 93:273-282

Swatdipong A, Vasemägi A, Koskinen MT, Piironen J, Primmer CR (2009) Unanticipated population structure of European grayling in its northern distribution: implications for conservation prioritization. Frontiers in Zoology 6

Swedish Agency for Marine and Water Management (2011) Statement on EU Commission Proposal for regulation of the European Parliament and of the Council establishing a multiannual plan for the Baltic salmon stock and the fisheries exploiting that stock. Swedish Agency for Marine and Water Management

Swedish Board of Fisheries (2010) EU strategy for the Baltic Sea Region Flagship project to ensure sustainable fisheries of Baltic Salmon: Links to biological diversity. Report from workshop. Helsinki 6-7 October, HELCOM headquarters

Swedish Salmon Research Institute (2000) Swedish Salmon Research Institute Annual report for year 2000. Swedish Salmon Research Institute, Älvkarleby ISSN 1401-5927 (in Swedish)

Tallmon DA, Luikart G, Waples RS (2004) The alluring simplicity and complex reality of genetic rescue. Trends in Ecology & Evolution 19:489-496

Tonteri A, Titov S, Veselov A, Zubchenko A, Koskinen MT, Lesbarrères D, Kaluzhin S, Bakhmet I, Lumme J, Primmer CR (2005) Phylogeography of anadromous and non-anadromous Atlantic salmon (*Salmo salar*) from northern Europe. Annales Zoologici Fennici 42:1-22

Tonteri A, Vasemägi A, Lumme J, Primmer CR (2010) Beyond MHC: signals of elevated selection pressure on Atlantic salmon (*Salmo salar*) immune-relevant loci. Molecular Ecology 19:1273-1282

Tonteri A, Veselov AJ, Titov S, Lumme J, Primmer CR (2007) The effect of migratory behaviour on genetic diversity and population divergence: a comparison of anadromous and freshwater Atlantic salmon *Salmo salar*. Journal of Fish Biology 70:381-398

Tymchuk WE, Sundström LF, Devlin RH (2007) Growth and survival trade-offs and outbreeding depression in rainbow trout (*Oncorhynchus mykiss*). Evolution 61:1225-1237

Utter F, Ryman N (1993) Genetic markers and mixed stock fisheries. Fisheries 18:11-21

Vasemägi A, Gross R, Paaver T, Kangur M, Nilsson J, Eriksson LO (2001) Identification of the origin of Atlantic salmon (*Salmo salar* L.) population in a recently recolonized river in the Baltic Sea. Molecular Ecology 10:2877-2882

Vasemägi A, Gross R, Paaver T, Koljonen ML, Nilsson J (2005a) Extensive immigration from compensatory hatchery releases into wild Atlantic salmon population in the Baltic Sea: spatio-temporal analysis over 18 years. Heredity 95:76-83

Vasemägi A, Gross R, Paaver T, Koljonen ML, Säisä M, Nilsson J (2005b) Analysis of gene associated tandem repeat markers in Atlantic salmon (*Salmo salar* L.) populations: implications for restoration and conservation in the Baltic Sea. Conservation Genetics 6:385-397

Verspoor E (1997) Genetic diversity among Atlantic salmon (*Salmo salar* L.) populations. ICES Journal of Marine Science 54:965-973

Verspoor E, Beardmore JA, Consuegra S, De Leaniz CG, Hindar K, Jordan WC, Koljonen ML, Mahkrov AA, Paaver T, Sanchez JA, Skaala O, Titov S, Cross TF (2005) Population structure in the Atlantic salmon: insights from 40 years of research into genetic protein variation. Journal of Fish Biology 67:3-54

Verspoor E, McCarthy EM, Knox D (1999) The phylogeography of European Atlantic salmon (*Salmo salar* L.) based on RFLP analysis of the ND1/16sRNA region of the mtDNA. Biological Journal of the Linnean Society 68:129-146

Wang JL, Caballero A (1999) Developments in predicting the effective size of subdivided populations. Heredity 82:212-226

Wang JL, Ryman N (2001) Genetic effects of multiple generations of supportive breeding. Conservation Biology 15:1619-1631

Waples RS (1999) Dispelling some myths about hatcheries. Fisheries 24:12-21

Wright S (1969) Evolution and the Genetics of Populations, Volume 2: Theory of Gene Frequencies. University of Chicago Press, Chicago

Öst T, Jansson H (1999) Investigation of salmon from the River Ljungan. Swedish Salmon Research Institute, Älvkarleby, Report to the Swedish Board of Fisheries (in Swedish)

Öst T, Jansson H (2001) Genetic follow-up of salmon and brown trout stocks reared for compensatory releases. Swedish Salmon Research Institute, Älvkarleby, Report to the Swedish Salmon Research Institute stakeholders

Websites:

www.vattenfall.se (Accessed November 2011-February 2012)
www.helcom.fi (Accessed November 2011-February 2012)
elurikkus.ut.ee (Accessed November 2011-February 2012)

Appendix

Status of Baltic salmon rivers in Sweden. The information is gathered from HELCOM (2011), personal contacts with Ingemar Perä (previous at the former Swedish Board of Fisheries), Jens Persson (Swedish University of Agricultural Sciences), Hans Olofsson (County Administrative Board of Västernorrland, previously at the Swedish Agency for Marine and Water Management) and Karl-Erik Nilsson (County Administrative Board of Norrbotten, previously at the Swedish Agency for Marine and Water Management), and our literature search in data bases and “gray literature” for genetic studies (see Table 3a and b).

River	**River number (according to Figure 1 and 2)**	**Wild salmon population and reproduction?**	**Hydropower developments?**	**Compensatory releases?**	**Any national protection?**	**Genetic references**
Alsterån	26	Very weak natural salmon stock with low reproduction	Yes	No	The river belongs to the Natura 2000 network.[1]	None
Byskeälven	8	Stable population of wild salmon	No	No	River Byskeälven is protected from hydropower production according to the Swedish Environmental Code (ch. 4, §6). The main river belongs to the Natura 2000 network. [1] River Byskeälven is classified as ”riksintresse för naturvård”.[2]	Koljonen 2006; Koljonen & McKinnel 1996; Koljonen & Pella 1997; Koljonen et al. 1999; Nilsson et al. 2001; Ryman & Ståhl 1981; Ståhl 1981, 1983, 1987; Säisä et al. 2005

River	River number (according to Figure 1 and 2)	Wild salmon population and reproduction?	Hydropower developments?	Compensatory releases?	Any national protection?	Genetic references
Dalälven	24	The stock is not self-sustaining and reproduces only at a small part of the river	Yes	190 000 salmon annually (Dalälven-strain) Year of court decision: 1993	Parts of the river and/or tributaries are protected from hydropower production according to the Swedish Environmental Code (ch. 4, §6).	Bourke et al. 1997; Jansson 1995; Jansson & Öst 1998; Koljonen 2006; Koljonen & McKinnel 1996; Koljonen & Pella 1997; Koljonen et al. 1999; Langefors 2005; Langefors et al. 1998, 2001; Nilsson et al. 2001; Säisä et al. 2005; Verspoor et al. 1999; Öst & Jansson 2001
Emån	25	Unique and self-sustaining wild salmon stock	Yes	No	River Emån is protected from construction of power stations according to the Swedish Environmental Code (ch. 4, §6). The main river belongs to the Natura 2000 network.[1]	Koljonen 2006; Nilsson et al. 2001; Ståhl 1983; Säisä et al. 2005

River	River number (according to Figure 1 and 2)	Wild salmon population and reproduction?	Hydropower developments?	Compensatory releases?	Any national protection?	Genetic references
Gideälven	17	Some natural reproduction, not self-sustaining	Yes	6 000 salmon annually (Skellefteälven-strain). Year of court decision: 1982 For compensatory releases in 2009, no information on stock in available.		None
Hörnån	14	No self-sustaining salmon population (most of the years there are no salmon at all)	No	No		None

River	River number (according to Figure 1 and 2)	Wild salmon population and reproduction?	Hydropower developments?	Compensatory releases?	Any national protection?	Genetic references
Indalsälven	20	No salmon reproduction	Yes	320 000 salmon annually (Indalsälven-strain). Year of court decision: 1973 According to court decision there is a possibility to change salmon to sea trout. Since 2009, 295 000 salmon are released annually.	Some tributaries belong to the Natura 2000 network.[1] Parts of the river and/or tributaries are protected from hydropower production according to the Swedish Environmental Code (ch. 4, §6).	Jansson 1995; Koljonen 2006; Koljonen & McKinnel 1996; Koljonen & Pella 1997; Koljonen et al. 1999; Nilsson et al. 2001; Ryman & Ståhl 1981; Ståhl 1983, 1987; Säisä et al. 2005; Väsemägi et al. 2005b; Öst & Jansson 1999, 2001
Kalixälven	3	Salmon population in good state	No	No	River Kalixälven was classified as “national river” in 1993.[3] The main river and its tributaries belong to the Natura 2000 network.[1] River Kalixälven is classified as ”riksintresse för naturvård”.[2]	Jansson 1993, 1995; Koljonen 2006; Koljonen & McKinnel 1996; Koljonen & Pella 1997; Koljonen et al. 1999; Nilsson et al. 2001; Ryman & Ståhl 1981; Ståhl 1981, 1983, 1987; Säisä et al. 2005

River	River number (according to Figure 1 and 2)	Wild salmon population and reproduction?	Hydropower developments?	Compensatory releases?	Any national protection?	Genetic references
Kågeälven	9	Yes	No	No		None
Ljungan	21	Genetically unique and self-sustaining wild stock	Yes	30 200 salmon or sea trout annually. Year of court decision: ? No releases of salmon are today taking place in Ljungan. During the last nine years, there have been compensatory releases of salmon only in 2004 (13 200 salmon of unknown stock).	Parts of the main river and parts of the tributary Gimån belong to the Natura 2000 network.[1] Parts of the river and/or tributaries are protected from hydropower production according to the Swedish Environmental Code (ch. 4, §6).	Jansson 1997; Koljonen 2006; Koljonen et al. 1999; Nilsson et al. 2001; Säisä et al. 2005; Öst & Jansson 1999, 2001

River	River number (according to Figure 1 and 2)	Wild salmon population and reproduction?	Hydropower developments?	Compensatory releases?	Any national protection?	Genetic references
Ljusnan	22	No natural reproduction	Yes	185 000 salmon annually (Ljusnan-strain). Year of court decision: 1980	Parts of the main river and the tributary Voxnan belong to the Natura 2000 network.[1] Parts of the river and/or tributaries are protected from hydropower production according to the Swedish Environmental Code (ch. 4, §6).	Jansson 1995; Koljonen 2006; Koljonen & McKinnel 1996; Koljonen & Pella 1997; Koljonen et al. 1999; Nilsson et al. 2001; Säisä et al. 2005; Väsemägi et al. 2005b; Öst & Jansson 1999, 2001

River	River number (according to Figure 1 and 2)	Wild salmon population and reproduction?	Hydropower developments?	Compensatory releases?	Any national protection?	Genetic references
Luleälven	5	No natural reproduction	Yes	550 000 salmon annually (Luleälven-strain). Year of court decision: 2006	Parts of the river and/or tributaries are protected from hydropower production according to the Swedish Environmental Code (ch. 4, §6).	Bourke et al. 1997; Jansson 1995; Koljonen 2006; Koljonen & McKinnel 1996; Koljonen & Pella 1997; Koljonen et al. 1999; Langefors 2005; Langefors et al. 1998, 2001; Nilsson et al. 2001; Verspoor et al. 1999; Väsemägi et al. 2005b; Ståhl 1983, 1987; Säisä et al. 2005; Öst & Jansson 2001

River	River number (according to Figure 1 and 2)	Wild salmon population and reproduction?	Hydropower developments?	Compensatory releases?	Any national protection?	Genetic references
Lögdeälven	16	Genetically unique and self-sustaining wild stock	No	No	The river is protected from construction of power stations according to the Swedish Environmental Code (ch. 4, §6). The entire river system belongs to the Natura 2000 network.[1] River Lögdeälven is classified as ”riksintresse för naturvård”.[2]	Koljonen 2006; Koljonen & McKinnel 1996; Koljonen & Pella 1997; Koljonen et al. 1999; Nilsson et al. 2001; Ryman & Ståhl 1981; Ståhl 1981, 1983, 1987; Säisä et al. 2005; Vasemägi et al. 2005a

River	River number (according to Figure 1 and 2)	Wild salmon population and reproduction?	Hydropower developments?	Compensatory releases?	Any national protection?	Genetic references
Moälven	18	Weak natural salmon population with low reproduction (reproduction areas too small)	Yes (fish can migrate at least 50 km).	No	River Moälven is protected from construction of power stations according to the Swedish Environmental Code (ch. 4, §6). The main river belongs to the Natura 2000 network.[1]	None
Mörrumsån	27	Wild self-sustaining salmon stock although the production has been reduced in the later years	Yes	No	River Mörrums is protected from construction of power stations according to the Swedish Environmental Code (ch. 4, §6). The main river belongs to the Natura 2000 network.[1]	Jansson & Öst 1998 Koljonen et al. 1999; Langefors 2005; Langefors et al. 1998, 2001; Nilsson et al. 2001; Säisä et al. 2005

River	River number (according to Figure 1 and 2)	Wild salmon population and reproduction?	Hydropower developments?	Compensatory releases?	Any national protection?	Genetic references
Piteälven	6	Yes	Only one hydropower plant in this river. Fish ladder exists.	No	River Piteälven was classified as "national river" in 1993.[3] The main river belongs to the Natura 2000 network.[1]	None
Rickleån	11	Weak but increasing salmon population that has earlier been supplemented by stocking	Yes	No		None

River	River number (according to Figure 1 and 2)	Wild salmon population and reproduction?	Hydropower developments?	Compensatory releases?	Any national protection?	Genetic references
Råneälven	4	Weak wild salmon population with a tendency to become stronger	No	No	River Råneälven is protected from construction of power stations according to the Swedish Environmental Code (ch. 4, §6). The main river belongs to the Natura 2000 network.[1]	Koljonen 2006
Sangisälven	2	No self-sustaining salmon population	Fish may pass the power plant by migrating through an old watercourse at high water. There are many migration obstacles (channels and culverts) in the river system (located mainly in the tributaries).	No		None

River	River number (according to Figure 1 and 2)	Wild salmon population and reproduction?	Hydropower developments?	Compensatory releases?	Any national protection?	Genetic references
Skellefteälven	10	No natural reproduction	Yes	118 500 salmon annually (Skellefteälven-strain). Year of court decision: 1962 For compensatory releases in 2002 and 2009, no information on stock is available.	Some tributaries belong to the Natura 2000 network.[1] Parts of the river and/or tributaries are protected from hydropower production according to the Swedish Environmental Code (ch. 4, §6).	Jansson 1995; Koljonen 2006; Koljonen & McKinnel 1996; Koljonen & Pella 1997; Koljonen et al. 1999; Nilsson 1997; Nilsson et al. 2001; Ståhl 1983, 1987; Säisä et al. 2005; Vasemägi et al. 2005a,b; Öst & Jansson 2001
Sävarån	12	A salmon population genetically separated from adjacent populations, the original salmon population has survived despite voluminous stockings (of e.g. the strains of Byskeälven).	The river is only marginally developed for hydropower.	No	River Sävarån is protected from construction of power stations according to the Swedish Environmental Code (ch. 4, §6). Parts of the main river belong to the Natura 2000 network.[1]	Nilsson et al. 2008

River	River number (according to Figure 1 and 2)	Wild salmon population and reproduction?	Hydropower developments?	Compensatory releases?	Any national protection?	Genetic references
Testeboån	23	The original population is extinct; there is however, some natural reproduction that is maintained by large continuous releases of reared fish.	Yes	No	Parts of the main river belong to the Natura 2000 network.[1]	None

River	River number (according to Figure 1 and 2)	Wild salmon population and reproduction?	Hydropower developments?	Compensatory releases?	Any national protection?	Genetic references
Torneälven	1	Yes (voluminous stockings of hatchery reared fish took place from the early 1980s until 2002)	Only one hydropower plant in the main river. The power station does not impede fish migration.	No	River Torneälven was classified as “national river” in 1993.[3] The main river and lakes belong to the Natura 2000 network.[1] River Torneälven is classified as ”riksintresse för naturvård”.[2]	Bourke et al. 1997; Jansson 1993, 1995; Jansson & Öst 1998; Koljonen 1989, 1995, 2006; Koljonen & McKinnel 1996; Koljonen & Pella 1997; Koljonen et al. 1999, 2002; Nilsson et al. 2001; Ryman & Ståhl 1981; Ryynänen & Primmer 2004; Ryynänen et al. 2007; Ståhl 1981, 1983, 1987; Tonteri et al. 2005, 2007, 2010; Vasemägi et al. 2005b; Verspoor et al. 1999

River	River number (according to Figure 1 and 2)	Wild salmon population and reproduction?	Hydropower developments?	Compensatory releases?	Any national protection?	Genetic references
Umeälven/ Vindelälven	13ab	Umeälven: no Vindelälven: yes	Yes (Vindeälven has only one hydropower plant, fish ladder exists).	94 000 salmon annually (Vindeälven-strain). Year of court decision: 1960	River Vindelälven was excepted from power plant developments in 1970 and classified as “national river” in 1993.[3] The entire River Vindelälven and the lower part of River Umeälven belong to the Natura 2000 network.[1] Rive r Vindelälven is to major parts classified as ”riksintresse för naturvård”.[2] Parts of the River Umeälven and/or tributaries are protected from hydropower production according to the Swedish Environmental Code (ch. 4, §6).	Jansson 1997; Jansson & Öst 1998; Koljonen 2006; Koljonen & McKinnel 1996; Koljonen & Pella 1997; Koljonen et al. 1999; Langefors et al. 1998, 2001, 2005; Nilsson 1997; Nilsson et al. 2001; Rynnänen et al. 2007; Tonteri et al. 2005, 2007, 2010; Säisä et al. 2005; Vasemägi et al. 2005a,b

River	River number (according to Figure 1 and 2)	Wild salmon population and reproduction?	Hydropower developments?	Compensatory releases?	Any national protection?	Genetic references
Åbyälven	7	Weak natural salmon stock with a stable increase during the latest years	Only one hydropower plant. Fish ladder exists.	No	River Åbyälven is protected from construction of power stations according to the Swedish Environmental Code (ch. 4, §6). Parts of the main river belong to the Natura 2000 network.[1]	Koljonen 2006
Ångermanälven	19	No natural reproduction	Yes	210 000 salmon annually (Ångermanälven-strain). Year of court decision: 1991	Parts of the river and/or tributaries are protected from hydropower production according to the Swedish Environmental Code (ch. 4, §6).	Jansson 1997; Jansson & Öst 1998; Koljonen 2006; Koljonen & McKinnel 1996; Koljonen & Pella 1997; Koljonen et al. 1999; Nilsson 1997; Nilsson et al. 2001; Vasemägi et al. 2005b; Säisä et al. 2005; Öst & Jansson 2001

River	River number (according to Figure 1 and 2)	Wild salmon population and reproduction?	Hydropower developments?	Compensatory releases?	Any national protection?	Genetic references
Öreälven	15	Natural reproduction if wild salmon, although the production is only 25% of what is expected	Yes (fish can migrate at least 70 km).	No	River Öreälven is protected from construction of power stations according to the Swedish Environmental Code (ch. 4, §6). The main river belongs to the Natura 2000 network.[1]	Koljonen 2006

[1] According to the Swedish Environmental Code ch. 7, § 28a. Special permissions are required if activities or arrangements which, in considerable ways, may affect the environment in areas belonging to the Natura 2000 network are carried out.

[2] According to the Swedish Environmental Code ch. 3, §6.

[3] Rivers classified as “national rivers” (rivers of national importance; *in Swedish: nationalälvar*) have legal protection from further hydropower developments according to the Swedish Environmental Code ch. 4, §6.

BONUS
SCIENCE FOR A BETTER FUTURE OF THE BALTIC SEA REGION

BaltGene
Baltic Sea Genetic Biodiversity

Sida
SWEDISH INTERNATIONAL
DEVELOPMENT COOPERATION AGENCY

norden
Nordic Council of Ministers

STOCKHOLMS UNIVERSITET
Stockholm
University