

University of Helsinki
Dissertationes Universitatis Helsingiensis
99/2023

Genomic approaches to guide the conservation and management of wild Atlantic salmon

Antti Miettinen

Doctoral Programme in Wildlife Biology (LUOVA)
Organismal and Evolutionary Biology Research Programme (OEB)
Faculty of Biological and Environmental Sciences
University of Helsinki, Finland

DOCTORAL DISSERTATION,
to be presented for public discussion with the permission of the Faculty of
Biological and Environmental Sciences of the University of Helsinki,
in Auditorium 2041, Biocenter 2, on the 5th of December, 2023 at 12 o'clock.

Helsinki 2023

Supervisors

Senior researcher Victoria Pritchard
Institute for Biodiversity and Freshwater Conservation
University of the Highlands & Islands, Inverness, United Kingdom

Professor Craig Primmer
Organismal and Evolutionary Biology Research Programme
Faculty of Biological and Environmental Sciences, Institute of Biotechnology
University of Helsinki, Finland

Thesis Advisory Committee

Docent Laura Kvist
Ecology and Genetics
Faculty of Science
University of Oulu, Finland

Research Professor Jaakko Erkinaro
Natural Resources Institute Finland (Luke)
Oulu, Finland

Reviewers

Professor Jouni Aspi
Ecology and Genetics
Faculty of Science
University of Oulu, Finland

Associate Professor Jens Carlsson
School of Biology and Environmental Science
University of Dublin, Ireland

Opponent

Professor Kathryn Elmer
Institute of Biodiversity, Animal Health & Comparative Medicine
College of Medical, Veterinary & Life Sciences
University of Glasgow
Glasgow, United Kingdom

Custos

Professor Craig Primmer
Organismal and Evolutionary Biology Research Programme
Faculty of Biological and Environmental Sciences, Institute of Biotechnology
University of Helsinki, Finland

Publisher: University of Helsinki
Series: *Dissertationes Universitatis Helsingiensis* 99/2023

ISBN 978-951-51-9538-8 (print)
ISBN 978-951-51-9539-5 (online)
ISSN 2954-2898 (print)
ISSN 2954-2952 (online)
PunaMusta, Joensuu 2023

The Faculty of Biological and Environmental Sciences uses the Ouriginal system (plagiarism recognition) to examine all doctoral dissertations.

CONTENTS

ABSTRACT	4
TIIVISTELMÄ	5
SAMMANFATTNING	6
LIST OF ORIGINAL PUBLICATIONS	7
AUTHOR CONTRIBUTIONS	7
ABBREVIATIONS	8
1. INTRODUCTION	9
1.1 Importance of intraspecific diversity.....	9
1.2 Genomic approaches in conservation.....	9
1.3 Atlantic salmon as a system to study local adaptation and human-induced evolution.....	11
1.3.1 Local adaptation, life-history diversity and their conservation implications.....	11
1.3.2 Genetic basis of life-history diversity.....	12
1.4 Baltic salmon.....	12
1.4.1 Knowledge gaps.....	14
2. AIMS OF THE THESIS	15
3. MATERIAL AND METHODS	16
3.1 Study area and sampling.....	16
3.1.1 Genetic baseline samples.....	16
3.1.2 Catch samples.....	17
3.2 Genetic markers.....	18
3.2.1 SNP panel development and use for genotyping of wild catch samples.....	19
3.3 Detection of candidate adaptive loci.....	20
4. RESULTS AND DISCUSSION	23
4.1 Upstream-downstream genetic divergence is linked to life-history variation.....	23
4.2 Signatures of local selection on adaptively relevant loci.....	24
4.3 Temporally varying selection pressures on adaptive loci imply potential for human-induced evolutionary change.....	27
4.4 Conservation and management implications.....	29
5. CONSIDERATIONS AND FUTURE DIRECTIONS	31
5.1 Genomic basis of local adaptation.....	31
5.2 Management-related perspectives.....	31
6. CONCLUSIONS	33
ACKNOWLEDGEMENTS	34
REFERENCES	36

ABSTRACT

Genetic variation is the foundation of all biological diversity. Documenting and understanding this variation and factors affecting it is paramount in the era of global biodiversity loss. This can be achieved through genomic approaches that provide insights into adaptively important genetic diversity. Such information can be used for efficient planning of conservation and management actions for natural populations. In particular, the discovery of large-effect loci linked to important life-history diversity allows studying the impacts of different selection pressures on ecologically relevant genetic variation.

In this thesis, I characterised fine-scale genetic structuring and putatively adaptive genetic variation in the largest Atlantic salmon (*Salmo salar*) stock in the Baltic Sea region, spawning in the Tornio and Kalix Rivers. Furthermore, I used an archive of tissue samples spanning 93 years (from 1928 to 2020) to examine how temporally varying fishing mortality may affect adaptively important genetic and life-history diversity in this actively exploited stock.

First, using 18 microsatellite markers, we found that upstream and downstream reaches of the large Tornio-Kalix River complex were genetically differentiated. This genetic structure was linked to life-history variation: migration timing at different life stages varied between salmon from upper and lower parts of the river system.

Second, we used a genome-wide SNP array of 60,252 markers to further explore the fine-scale population structure and to detect potentially adaptive genetic variation in the Tornio-Kalix. We identified further population genetic substructuring and strong candidates for genomic regions putatively under locally divergent selection. These regions contained genes previously associated with major life-history variation, such as migration and maturation timing of Atlantic salmon.

Third, we developed a genotyping-by-sequencing SNP panel to monitor spatiotemporal variation in harvesting pressures imposed by commercial and recreational fisheries on adaptive genetic variation and different subpopulations of the Tornio-Kalix stock. We demonstrated that both coastal and river fisheries caught more salmon of upstream origin in the early than late fishing season. We also found that the frequency of a genetic variant strongly associated with older age at maturity in Atlantic salmon drastically decreased in the catches over the fishing season. This indicates that temporal variation in harvesting mortality has the potential to cause evolutionary changes in salmon life-history diversity.

Together, these results provided valuable information for guiding the conservation and management of wild Atlantic salmon. This thesis thus provides a tangible example of using genetic and genomic approaches to infer and monitor ecologically important genetic variation in nature and to help mitigate human impacts on it.

TIIVISTELMÄ

Perinnöllinen muuntelu on kaiken biologisen monimuotoisuuden perusta. Tämän muuntelun ja siihen vaikuttavien tekijöiden selvittäminen on ensiarvoisen tärkeää maailmanlaajuisen luontokadon aikakaudella. Genomiset menetelmät tarjoavat keinon tutkia ja ymmärtää eliöiden sopeutumisen kannalta tärkeää ”adaptiivista” geneettistä monimuotoisuutta, kuten perimän alueita, jotka vaikuttavat voimakkaasti muunteluun eliöiden elinkierto- ja elinpiirteissä. Tämä mahdollistaa tutkimukset erilaisten valintapaineiden vaikutuksista ekologisesti tärkeään geneettiseen monimuotoisuuteen. Tietoa voi käyttää luonnonpopulaatioiden suojelun ja hoidon suunnittelussa.

Tutkin tässä väitöskirjassa Itämeren alueen pohjoisosassa, Tornionjoessa ja Kalixjoessa kutevan Atlantin lohien (*Salmo salar*) kannan geneettistä rakennetta ja adaptiivista geneettistä muuntelua. Käytin lisäksi 93 vuoden ajalta (1928–2020) kerättyä näytearkistoa tästä Itämeren suurimmasta lohikannasta selvittääkseni, miten ajallisesti vaihteleva kalastuskuolleisuus saattaa vaikuttaa kannan adaptiivisesti tärkeään geneettiseen monimuotoisuuteen ja sitä kautta elinkierto- ja elinpiirteisiin.

Havaitsimme 18:aa mikrosatelliittimarkkeria käyttämällä Tornionjoen-Kalixjoen ylä- ja alajuoksujen lohien eroavan toisistaan geneettisesti. Tämä geneettinen rakenne oli yhteydessä muunteluun elinkierto- ja elinpiirteissä: ylä- ja alajuoksulta lähtöisin olevat lohet vaelsivat keskenään eri aikoihin eri elinkierron vaiheissa.

Käytimme lisäksi 60 252 SNP-markkerin kokoelmaa Tornionjoen-Kalixjoen populaatorakenteen tarkemmaksi tutkimiseksi sekä jokisysteemin lohikannassa mahdollisesti esiintyvän adaptiivisen geneettisen muuntelun havaitsemiseksi. Tunnistimme osapopulaatioita ja perimän alueita, joihin paikalliset valintapaineet mahdollisesti vaikuttavat. Nämä alueet sisälsivät geenejä, jotka on yhdistetty vaihteluun esimerkiksi lohien vaelluksen ja sukukypsyyden ajoituksessa.

Kehitimme myös ns. genotyping by sequencing -menetelmään perustuvan SNP-markkerikokoelman seurataksemme, miten ajallinen ja paikallinen vaihtelu kalastuksessa voi vaikuttaa Tornionjoen-Kalixjoen lohien eri osakantoihin ja adaptiiviseen geneettiseen muunteluun. Osoitimme, että yläjuoksulta lähtöisin olevien lohien osuus saaliissa oli sekä rannikko- että jokikalastuksessa suurempi alku- kuin loppukaudella. Havaitsimme myös, että Atlantin lohien vanhaan sukukypsyydeseen ja siten suureen kokoon vahvasti kytkeytyvä geenimuoto oli huomattavasti yleisempi alku- kuin loppukauden saaliissa. Tämä viittaa siihen, että ajallinen vaihtelu kalastuskuolleisuudessa voi potentiaalisesti aiheuttaa evolutiivisia muutoksia lohien elinkierto- ja elinpiirteissä.

Tämä väitöskirja on konkreettinen esimerkki luonnossa esiintyvän, ekologisesti tärkeän perinnöllisen muuntelun tunnistamisesta ja seurannasta geneettisin ja genomisin menetelmin. Työn tuottamaa tietoa voi käyttää lieventämään ihmistoiminnan vaikutuksia tähän muunteluun. Tulokset hyödyttävät Itämeren lohien suojelua ja kantojen hoitoa.

SAMMANFATTNING

Genetisk variation utgör grunden för all biologisk mångfald. Att dokumentera och förstå denna variation samt bakomliggande faktorer är av största vikt under eran av global förlust i den biologiska mångfalden. Det här kan uppnås med genomiska metoder som ger kännedom i adaptivt viktig genetisk variation. Den erhållna kunskapen kan användas för att effektivt planera bevarandet och förvaltningen av vilda populationer. Fynden av framför allt loci med stor effekt på den viktiga livshistoriemångfalden gör det möjligt att forska i effekterna av olika selektionstryck på ekologiskt relevant genetisk variation.

I denna avhandling karaktäriserar jag den detaljerade genetiska strukturen och förmodade adaptiva genetiska variationen i Östersjöregionens största laxbestånd som leker i Torne- och Kalixälvarna. Med hjälp av arkiverade vävnadsprov samlade över en tidsperiod på 93 år (från 1928 till 2020) undersökte jag också hur tidsmässigt varierande fiskedödlighet påverkar adaptivt viktig genetisk och livshistorisk mångfald i beståndet som aktivt utnyttjas.

Först fann vi med hjälp av 18 mikrosatellitmarkörer att Torne och Kalix älvsystems uppströms- och nedströmslekande laxar var genetiskt differentierade. Den genetiska strukturen var kopplad till livshistorisk variation: olika livsstadiers vandringstidpunkt skilde sig mellan de övre och nedre delarna av älvsystemet.

För det andra utnyttjade vi en genomomfattande SNP-array bestående av 60 252 markörer för att mer detaljerat utforska populationsstrukturen och finna potentiellt adaptiv genetisk variation i Torne och Kalix älvsystem. Vi identifierade en genetisk substruktur samt starka kandidater för genomiska regioner under lokalt divergerande urval. Regionerna innefattade gener som tidigare förknippats med variation i livshistoriska egenskaper hos atlantisk lax såsom tidpunkterna för vandring och könsmognad.

För det tredje utvecklade vi en SNP-panel för genotypning genom sekvensering med ändamålet att observera hur spatiotemporal variation i fisketryck från både kommersiellt fiske och fritidsfiske påverkar adaptiv genetisk variation och olika delpopulationer i Torne och Kalix älvsystem. Vi visade att både kust- och flodfiskefångsten bestod till högre grad av uppströmslekande lax under den tidiga jämfört med den sena fiskesäsongen. Vi fann också att frekvensen av en genetisk variant som starkt förknippats med högre könsmognadsålder hos lax minskade drastiskt bland fångsten under fiskesäsongen. Det här antyder att tidsmässig variation i fiskedödlighet har potential att orsaka evolutionära förändringar i laxens livshistorievariation.

Tillsammans gav de erhållna resultaten värdefull information som kan användas för att vägleda bevarandet och förvaltningen av vild lax. Avhandlingen är således ett konkret exempel på hur genetiska och genomiska metoder kan användas för att finna och uppfölja ekologiskt viktig genetisk variation i naturen och för att minska människans inverkan på den.

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following publications, referred to in the text by their Roman numerals:

I Miettinen A, Palm S, Dannewitz J, Lind E, Primmer CR, Romakkaniemi A, Östergren J & Pritchard VL (2020). A large wild salmon stock shows genetic and life history differentiation within, but not between, rivers. *Conservation Genetics* 22, 35–51. doi: <https://doi.org/10.1007/s10592-020-01317-y>

II Miettinen A, Dannewitz J, Palm S, Pashay Ahi E, Romakkaniemi A, Vähä V, Östergren J, Primmer CR & Pritchard VL (2023). Loci associated with maturation, migration and appetite control are linked with signals of fine-scale local selection in a large Atlantic salmon population. *Manuscript*.

III Miettinen A, Romakkaniemi A, Dannewitz J, Pakarinen T, Palm S, Persson L, Östergren J, Primmer CR & Pritchard VL (2023). Temporal allele frequency changes reveal potential fishing impacts on salmon life history diversity. Manuscript submitted to and under revision in *Evolutionary Applications*.

AUTHOR CONTRIBUTIONS

Role	Chapter I	Chapter II	Chapter III
Conceptualisation	AR, JD, JÖ, SP	AM, CRP, VLP	AM, AR, CRP, TP, VLP
Data collection/collation	AR, JÖ	AR, JD, JÖ, SP, VV	AM, AR, JD, JÖ, LP, SP, TP
Laboratory work	EL	AM	AM
Methodology	AM, EL, JD, JÖ, SP, VLP	AM, VLP	AM, VLP
Data analysis	AM, JD, JÖ, SP, VLP	AM, EPA	AM, VLP
Visualisation	AM, VLP	AM	AM, VLP
Writing*	AM, AR, SP, VLP	AM	AM, VLP

* Along with comments/contributions from other authors.

Note: The author order in the table above is alphabetical. Full author names are listed below.

AM: Antti Miettinen	AR: Atso Romakkaniemi	CRP: Craig R. Primmer	EPA: Ehsan Pashay Ahi
EM: Emma Lind	JD: Johan Dannewitz	JÖ: Johan Östergren	LP: Lo Persson
SP: Stefan Palm	TP: Tapani Pakarinen	VV: Ville Vähä	VLP: Victoria L. Pritchard

ABBREVIATIONS

FIE = Fisheries-induced evolution

GEA = Genotype-environment association

GSI = Genetic stock identification

GT-seq = Genotyping-in-thousands by sequencing

IBD = Isolation by distance

PCA = Principal component analysis

RDA = Redundancy analysis

SNP = Single nucleotide polymorphism

XP-EHH = Cross-population extended haplotype homozygosity

1. INTRODUCTION

1.1 Importance of intraspecific diversity

Anthropogenic drivers such as habitat loss and degradation, climate change and overexploitation of natural populations are behind the rapid and ongoing loss of global biodiversity (IPBES 2019). Although most research on declining biodiversity has focused on the species level, variation within species (intraspecific diversity) can be as extreme as that between them (Des Roches *et al.* 2018). Extirpation and shrinking sizes of wild populations and human-induced selection are driving rapid declines in intraspecific diversity (e.g. Pinsky and Palumbi 2014; Mimura *et al.* 2017).

Genetic variation is the cornerstone of biodiversity, as it provides the raw material for the evolution of populations (Frankham *et al.* 2017). Genetic diversity that underlies fitness-related traits (adaptive genetic diversity) is central for the potential of populations to adapt to changing environmental conditions, and consequently expected to promote long-term persistence of populations (Hilborn *et al.* 2003). Diversity in ecologically important traits, such as life-history strategies, can also promote the stability of populations by buffering them against environmental change and stochasticity (Schindler *et al.* 2010; Gharrett *et al.* 2013; Hoelzel *et al.* 2019; Cordoleani *et al.* 2021; Carvalho *et al.* 2023).

Genetic diversity has declined by an estimated 6% in wild populations since the Industrial Revolution (Leigh *et al.* 2019). This is concerning as the adaptive potential provided by intraspecific genetic variation is particularly important during the rapid, global environmental changes in the Anthropocene (Jensen *et al.* 2022b). Genetic diversity is still mostly overlooked in biodiversity assessments and policy (Laikre 2010; Frankham *et al.* 2017; Hoban *et al.* 2021), but efforts have been made on national (e.g. Jarkko *et al.* 2019) and international levels (e.g. Hoban *et al.* 2020) to improve its recognition as essential for conservation and management applications. A major limiting factor in integrating genetic diversity into policy has been the lack of population-level genetic data from most species (Schmidt *et al.* 2023). Urgent action is therefore needed to document and preserve the existing genetic diversity in a broad range of taxa.

1.2 Genomic approaches in conservation

Population genetic and genomic methods help us understand important properties of natural populations, such as their size, connectivity and evolutionary processes affecting intraspecific diversity (Hohenlohe *et al.* 2021). For example, these methods can pinpoint genetic structuring of populations that is crucially valuable information for the effective conservation and management of threatened and/or exploited species (e.g. Quintela *et al.* 2020). The relatively new field of conservation genetics and genomics aims to bridge the gap between academic research and on-site needs of conservation, by incorporating insights from genetic studies into biodiversity policies (Shafer *et al.* 2015).

Genomic approaches allow the identification of genome regions contributing to adaptive phenotypic variation (Shafer *et al.* 2015). This is a core focus of evolutionary biology, as characterising the genomic basis of traits, the distribution of adaptive variation across the genome and its recurrence in different evolutionary lineages can help us understand how biological diversity arises and is maintained. Knowledge of adaptively important genetic variation is also essential for conservation and management, as it can highlight loci, ecological factors and phenotypes relevant to population persistence (Kardos and Shafer 2018). In general, high-throughput genomic datasets can provide natural resource managers relevant information and practical methods for promoting the long-term viability of populations (Mamoozadeh *et al.* 2023).

Signatures of adaptive genetic variation can be identified by genome scans that examine spatially varying allele frequencies potentially shaped by selection (reviewed e.g. by Hoban *et al.* 2016). Potentially adaptive genetic variation can also be identified by landscape genomic approaches or genome-wide association studies (GWAS) that detect correlations between genetic and environmental or phenotypic variation (Rellstab *et al.* 2015). These kinds of approaches have identified loci of large effect associated with variation in important life-history traits, such as the horn type of Soay sheep (*Ovis aries*) (Johnston *et al.* 2013), salmonid maturation and migration timing (Barson *et al.* 2015; Hess *et al.* 2016; Prince *et al.* 2017; Pearse *et al.* 2019), gill-raker count in Alpine whitefish (genus *Coregonus*) (De-Kayne *et al.* 2022), and mating behaviour in ruff (*Philomachus pugnax*) (Lank *et al.* 1995, 2013). Information of such adaptive genetic variation can be applied in delineating population or conservation units, predicting their responses to anthropogenic effects, and even in gene-targeted management to preserve the adaptive diversity of populations (Funk *et al.* 2012; Shafer *et al.* 2015; Kardos and Shafer 2018; Thompson *et al.* 2019; Waples *et al.* 2022).

The field of temporal genomics makes use of samples from multiple time points to examine evolutionary change, often with the focus of assessing anthropogenic impacts on genetic diversity (e.g. Pinsky *et al.* 2021; Clark *et al.* 2023). Genotyping historical samples can provide crucial information for conservation, for example about levels of intraspecific diversity or extent of population structure before large-scale human activities (Nielsen and Hansen 2008; Mondol *et al.* 2013; Habel *et al.* 2014; Nakahama 2021; Jensen *et al.* 2022b; Heino *et al.* 2023). As an example, studying temporal genetic variation in functionally important large-effect loci can illuminate potential evolutionary impacts of anthropogenic selection pressures on ecologically relevant traits across time (e.g. (Czorlich *et al.* 2018a, 2022; Thompson *et al.* 2019; Campbell-Staton *et al.* 2021; Jensen *et al.* 2022a). Temporal changes in such loci can provide information about the adaptive potential of populations and may be used to guide conservation and management actions for exploited populations (reviewed in Waples *et al.* 2022; Benham and Bowie 2023).

Harvesting, such as fishing, has the potential to influence life-history traits of exploited populations (Heino *et al.* 2015). Fisheries-induced evolution (FIE) has been a long-standing concern: certain harvesting strategies, especially those targeting larger and older fish, have been expected to ultimately lead to reduced yields through the assumed evolutionary impact on fish size and age at maturity (Rutter 1902; Handford *et al.* 1977). Selection induced by fisheries is thus an unintended form of artificial selection

(Heino *et al.* 2015) with potentially detrimental consequences for the diversity of fish stocks. Although selection against larger and older fish has been shown to reduce mean size and age at maturity over time (Allendorf and Hard 2009; van Wijk *et al.* 2013; Uusi-Heikkilä *et al.* 2015), empirical evidence of FIE in wild populations is scarce (Hutchings and Kuparinen 2020). In addition, fisheries management is almost exclusively based on demographic considerations and ignores possible effects of FIE on exploited stocks (Allendorf and Hard 2009). Genetic monitoring of fisheries can improve our understanding of anthropogenic evolutionary changes by detecting possible adaptive responses of exploited stocks to harvesting selection.

1.3 Atlantic salmon as a system to study local adaptation and human-induced evolution

1.3.1 Local adaptation, life-history diversity and their conservation implications

Atlantic salmon (*Salmo salar*, Salmonidae) is an ecologically, culturally and economically important fish species across its range (Myrvold *et al.* 2019). It has been heavily impacted by human activities and is increasingly threatened by climate change (Jonsson and Jonsson 2009; Thorstad *et al.* 2021).

Atlantic salmon exhibits wide variation in its life-history characteristics, such as in the timing of maturation and seasonal migrations. In general, anadromous Atlantic salmon spend their first years in fresh water, from where they migrate to the sea, and return one to multiple years later to spawn (hereafter “age at maturity” or “sea age”) near their natal freshwater location (Thorstad *et al.* 2011). The precise homing behaviour promoting reproductive isolation (Quinn 1993) provides opportunities for locally adaptive differentiation over fine spatial scales. Salmonids indeed frequently exhibit pronounced geographic population structuring and fine-scale local adaptation (Fraser *et al.* 2011; Primmer 2011), contributing to the broad intraspecific diversity. Coupled with ample genomic resources, this makes Atlantic salmon a suitable model for exploring fine-scale adaptive genetic variation, of which examples have been putatively identified in different lineages of the species (Pritchard *et al.* 2018; Wellband *et al.* 2018; Watson *et al.* 2022).

Variation in age at maturity in Atlantic salmon is an important trait from ecological and economical perspectives (reviewed in Mobley *et al.* 2021). Atlantic salmon of an older sea age are larger and have higher reproductive success than younger and smaller individuals, and their proportion can positively correlate with the genetic diversity of salmon stocks (Vähä *et al.* 2007). However, maturation at an older age decreases the probability of survival to reproduction. Furthermore, large salmon are particularly prized catches for fishers and thus attract fishing tourism (Anderson and Lee 2013; Pokki *et al.* 2018; Myrvold *et al.* 2019). Older-maturing Atlantic salmon have generally become rarer (Chaput 2012), which has raised conservation concern.

Age at maturity is also linked to seasonal timing of spawning migration: old and large Atlantic salmon tend to return from the sea to fresh water early in the migration season (Shearer 1990; Jokikokko *et al.* 2004; Niemelä *et al.* 2006; Harvey *et al.* 2017). Also, Atlantic salmon spawning in upstream parts of river systems are often old and enter

fresh water early during the spawning migration season (e.g. Stewart *et al.* 2002). This implies that variation in seasonal timing of fishing may impose differential selective pressures on different life-history strategies and genetic subpopulations of Atlantic salmon stocks. This is important to note for management as variation in age at maturity and timing of return migration contribute significantly to the portfolio of life-history diversity and resilience of salmon populations (Quinn *et al.* 2016; Erkinaro *et al.* 2019; Tamario *et al.* 2019; Jacobson *et al.* 2020).

1.3.2 Genetic basis of life-history diversity

Variation in age at maturity across European phylogeographic lineages of Atlantic salmon is largely explained by a single locus around the *vgll3* (*vestigial-like family member 3*) gene on chromosome 25 (Ayllon *et al.* 2015; Barson *et al.* 2015). Salmon carrying the *vgll3* allele associated with “later” or “older” age at maturity (“*vgll3**L”) tend to spend more years at sea before returning to spawn than salmon carrying the “earlier” maturation allele (“*vgll3**E”) (Barson *et al.* 2015).

A second locus, associated with the *six6* (*SIX homeobox 6*) gene on chromosome 9, may also contribute to Atlantic salmon age at maturity (e.g. Sinclair-Waters *et al.* 2020, 2022). Additionally, variation at this locus is linked to return migration timing of Atlantic salmon (Cauwelier *et al.* 2018; Pritchard *et al.* 2018).

The link between genetic and phenotypic variation in adaptively important traits is often unknown, which has limited the application of adaptive genetic variation in conservation (Kardos and Shafer 2018). Large-effect loci linked with ecologically important life-history traits, such as *vgll3* and *six6*, offer opportunities to monitor how selection targets adaptive genetic variation, and how populations respond to it. Genetic monitoring of such loci thus allows studying how anthropogenic drivers, such as fishing regimes, affect intraspecific diversity. Atlantic salmon is therefore a rare example of a species that allows studying contemporary evolution by monitoring of temporal changes in specific loci. Recent studies have found rapid declines in salmon populations’ mean maturation age along with decreases in the frequencies of the *vgll3**L and/or *six6**L variants, demonstrating that the observed age at maturity shifts have been an evolutionary response (Czorlich *et al.* 2018b, 2022; Jensen *et al.* 2022a).

1.4 Baltic salmon

The Baltic Sea in northern Europe hosts a distinct phylogeographic lineage of Atlantic salmon (Bourret *et al.* 2013; hereafter “Baltic salmon”). People in this region give salmon high cultural value (Autti and Karjalainen 2012) and have used salmonids for food for millennia (Butler *et al.* 2019). In the past century, hydropower construction, pollution and overfishing have extirpated Baltic salmon from approximately two thirds of the rivers they historically spawned in (Karlsson and Karlström 1994; Romakkaniemi *et al.* 2003; Palmé *et al.* 2012). In addition, gene flow due to stocking of hatchery-produced salmon has homogenised Baltic salmon populations (both within and among rivers), raising concern for the remaining populations’ ability to adapt to changing environmental conditions (Östergren *et al.* 2021). Due to these reasons, Baltic salmon are currently considered threatened (VU; vulnerable; HELCOM Red List, HELCOM 2013).

Most Baltic salmon today originate from wild rivers and hatcheries in the Gulf of Bothnia, in the northernmost part of the Baltic Sea. After leaving fresh water, salmon from this region migrate to feed in the southern Baltic Sea. When reaching sexual maturation, the adult salmon migrate north towards their natal rivers (Figure 1). While on this spawning migration during spring and summer months, the salmon are harvested by fisheries (ICES 2020, 2023; Jacobson *et al.* 2020; Whitlock *et al.* 2021).

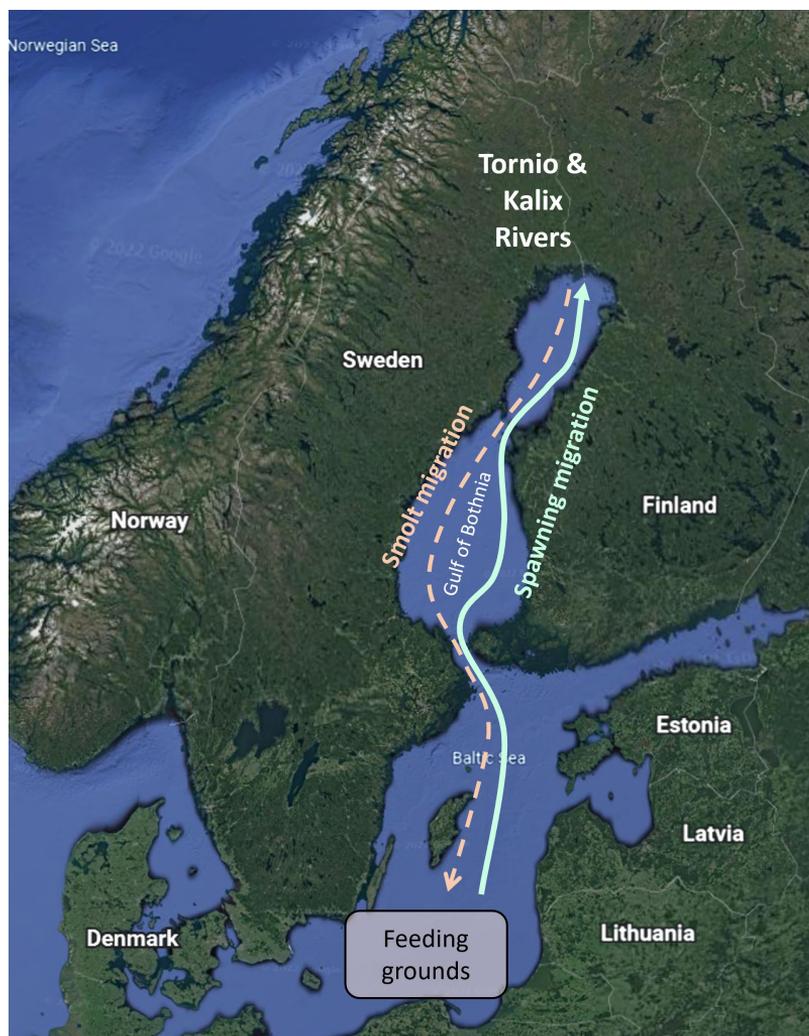


Figure 1. Main estimated migration routes of salmon originating from the Tornio-Kalix River system (based on Ikonen 2006; Whitlock *et al.* 2018). Google Earth was used to create the underlying map that includes data from Google, Landsat/Copernicus, Data SIO, NOAA, U.S. Navy, NGA, GEBCO, IBCAO, and U.S. Geological Survey.

The largest remaining wild Baltic salmon stock spawns in the northernmost part of the region, in the unregulated Tornio (Torne in Swedish, Duortnoseatnu in Northern Sámi) and Kalix (Gáláseatnu in Northern Sámi) Rivers in Finland and Sweden (ICES 2023). A natural bifurcation connects these two large neighbouring rivers, essentially making them one large complex. Salmon from the Tornio and Kalix migrate through all the

major salmon fishing areas in the Baltic Sea and are thus heavily exploited by marine fisheries (ICES 2023). They are also valuable for local fishers and tourist anglers along the rivers, benefitting the local economy (Pohja-Mykrä *et al.* 2018). Concerns for the long-term future of the salmon stock have been raised already in the 19th century (Kokko 1864).

Current salmon fishing regulations in the Baltic Sea are a controversial topic. The marine fishery is the largest commercial sea harvest of Atlantic salmon permitted in the world (ICES 2023), and targets salmon of mixed origin (i.e. the catches comprise salmon from multiple stocks) (Jacobson *et al.* 2020). In 2017, Finland advanced the allowed start date of the coastal fishery, allowing a limited amount of salmon harvest in the early summer. This “advanced early-season fishing” has sparked discussions about whether it allows excessive harvesting of large, older-maturing salmon that tend to migrate earlier in the season, and ultimately leads to a reduction in mean age at maturity of Baltic salmon stocks. This concern may be particularly relevant for the Tornio-Kalix salmon that are harvested primarily along the eastern side of the Gulf of Bothnia during their spawning migration (Whitlock *et al.* 2018).

1.4.1 Knowledge gaps

Efficient management of exploited fish stocks requires an understanding of their underlying population structure and can benefit from knowledge of intraspecific diversity (e.g. Bekkevold *et al.* 2020; Fuentes-Pardo *et al.* 2023). However, prior to this thesis, within-river neutral or adaptive genetic differentiation of Baltic salmon had not been assessed at fine spatial scales or by using genome-wide marker sets. Earlier studies of temporal and spatial variation of Baltic salmon populations in mixed-stock coastal catches (e.g. Koljonen and McKinnell 1996; Koljonen 2006) had therefore not been able to assess harvesting mortality faced by within-river subpopulations, or selective pressures exerted on adaptive genetic variation. Consequently, Baltic salmon have thus far been managed on the river level, without considerations of potential genetic structure and adaptive diversity within rivers.

To improve our understanding of the diversity and relevant biological units in this salmon lineage, this thesis investigated fine-scale population substructuring, adaptive differentiation and their potential drivers, to ultimately guide effective conservation and management of wild salmon. Through monitoring of temporal genetic variation in salmon catches, this work specifically focused on exploring the potential evolutionary impacts of fishing on salmon life-history diversity. This included assessing whether fishing particularly in the early season targets adaptively important genetic variation in Baltic salmon.

2. AIMS OF THE THESIS

In this thesis, I aimed to:

- 1) characterise the fine-scale population genetic structure of the largest Baltic salmon stock (spawning in the Tornio-Kalix River complex) and its associations with life-history variation (Chapters I and II),
- 2) uncover potential adaptive genetic variation in the Tornio-Kalix salmon (Chapter II),
- 3) elucidate how fishing may affect this genetic variation and the phenotypic traits it underlies (Chapter III), and ultimately to
- 4) guide the conservation and management of wild Atlantic salmon in the Baltic Sea region (Chapters I-III).

The broader objectives of this work were to improve our understanding of neutral and adaptive genetic diversity and its potential drivers in a large Atlantic salmon stock, and by monitoring adaptively important loci, to infer possible evolutionary responses of salmon to human-induced selective pressures.

Overall, this thesis represents an effort to bridge the gap between academic research and practical conservation. The process of translating the outcomes of this academic groundwork towards concrete management actions is outlined below (Figure 2).

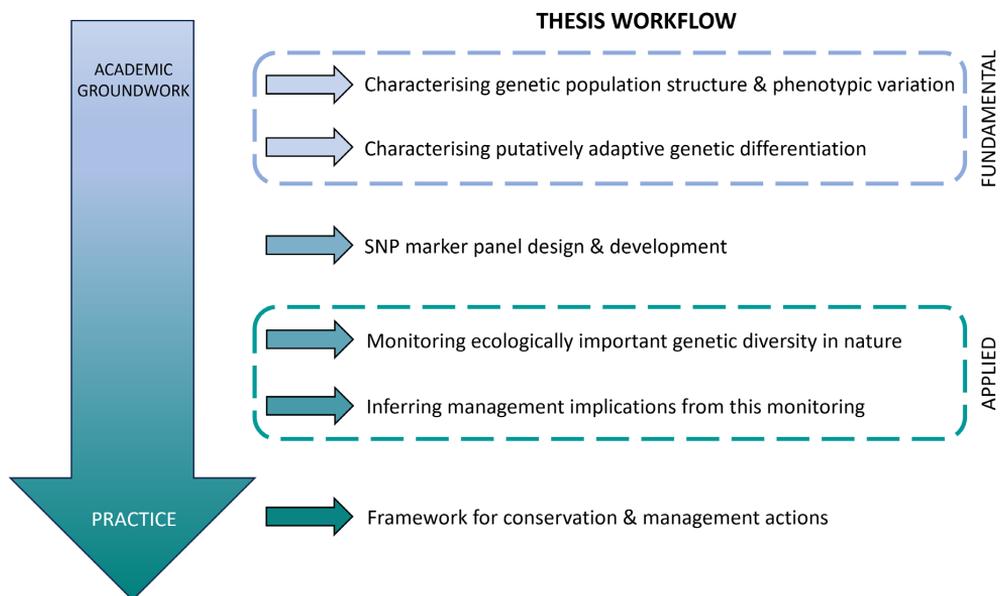


Figure 2. Diagram describing how genetic information generated in Chapters I and II of this thesis was used as a basis for developing a method (SNP marker panel) that was utilised in addressing applied management questions (Chapter III). The colour gradient corresponds to the transition from more fundamental to applied research.

3. MATERIAL AND METHODS

3.1 Study area and sampling

This thesis made use of Atlantic salmon samples of different life stages from the Baltic Sea region, with particular focus on the largest wild Baltic salmon stock that spawns in the Tornio and Kalix Rivers in Finland and Sweden. The Tornio and Kalix are among the largest undammed rivers in northern Europe (Tornio: length 522 km, watershed area 40,157 km²; Kalix: length 461 km, watershed area 23,600 km²). They are located in a terrain that ranges from a boreal zone to a subarctic headwater zone (Romakkaniemi *et al.* 2003; HELCOM 2011). The two rivers have their mouths located c. 50 km apart, and flow into the northernmost part of the Gulf of Bothnia in the Baltic Sea. A natural bifurcation (Tärendö River) ca. 200-250 km upstream of the river mouths connects the two rivers.

3.1.1 Genetic baseline samples

Genetic baseline samples for the studies in this thesis were collected in 2004-2019 from five wild rivers (Kalix, Råne, Simo, Tornio and Vindel) and six stocks of reared origin (Ii, Kymi/Neva, Lule, Oulu, Simo and Tornio broodstocks). These samples were used to i) study the population structure of northern Baltic salmon stocks (Chapters I-III), ii) identify putatively adaptive genetic variation in the Tornio-Kalix River system (Chapter II), and iii) allow genetic stock identification (GSI) of mixed-stock salmon catches in coastal and river fisheries (Chapters I and III).

Altogether, we used 1,149 unique baseline individuals, of which 274 were shared among all chapters (Table 1). Chapter III contained baseline samples from the five wild rivers and six stocks of reared origin mentioned above (Figure 3a), whereas Chapters I and II used only samples from the Tornio and Kalix Rivers (Figure 3b). Chapter I contained the largest Tornio-Kalix baseline (n = 749), of which we used a subset (n = 274) in Chapter II. We complemented this subset of Chapter I samples by adding three additional electrofishing sites (n = 54 individuals) in Chapters II and III, to improve the spatial resolution of sampling in the upper parts of the Tornio River system. In Chapters II and III, we also replaced Chapter I samples from two sites (Ka6 and Ka7, collected in 2012) with other individuals from the same sites (n = 33, collected in 2015), because the original tissue samples used in Chapter I were not available anymore for Ka6 and Ka7. We assumed the population structure in the system between 2012 and 2015 to be relatively stable, which is supported by the similar patterns of genetic divergence of Ka6 and Ka7 to other sites in the microsatellite and SNP datasets (Chapters I and II).

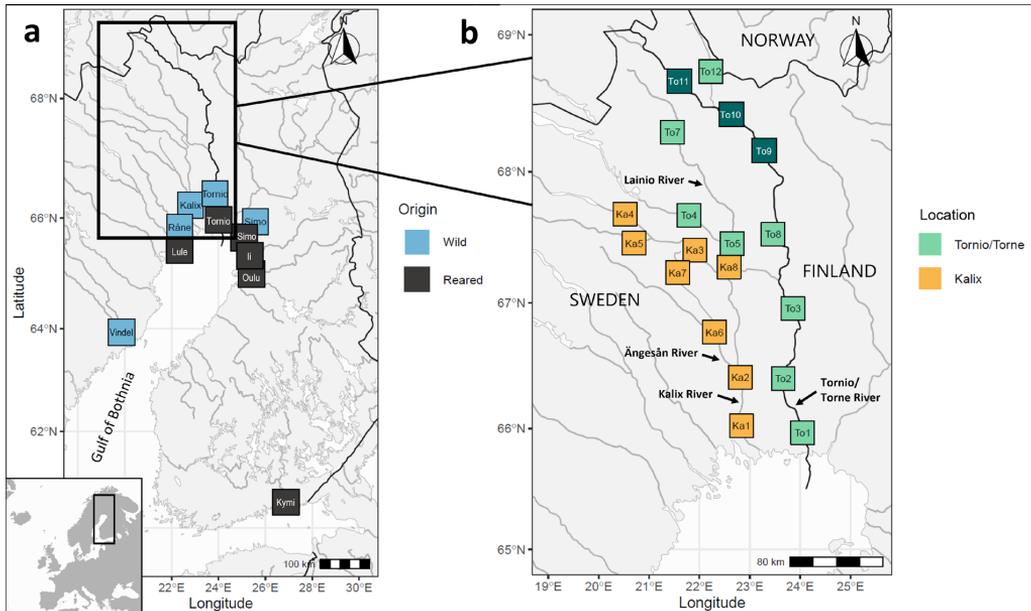


Figure 3. The geographic origin of baseline samples (Chapters I-III), showing the **a** broad locations of origin of the whole baseline (Chapter III), and **b** sampling of juveniles from the Tornio-Kalix system (Chapters I-III). Sites coded with darker green and a white font were only used in Chapters II and III. The darker lines depict national borders, including the Tornio River that flows on the border of Finland and Sweden.

3.1.2 Catch samples

In this thesis, we used an archive of Baltic salmon scale samples collected over 93 years (1928 to 2020) from commercial and recreational fisheries targeting adult salmon on their spawning migration. Adult catch samples from the Tornio River in 2009-2010 ($n = 287$) were collected from one 70-kilometre river stretch and were used only in Chapter I (Table 1), whereas three Tornio River stretches were used in Chapter III, providing a more complete picture of spatiotemporal fishing patterns in the region. The samples were selected to be representative of the total catch throughout the fishing seasons, without consideration of sex or age at maturity. Furthermore, in Chapter I we used smolts collected in 2011 from a trap located at the Tornio River mouth ($n = 196$). Altogether, we analysed genotypes of 3,228 smolt and adult catch samples across all chapters. The catch samples (Figure 4) were used for i) understanding patterns of temporal variation in stock composition of smolt and adult migrations within seasons (Chapters I and III), and ii) monitoring how fishing may target life-history loci within fishing seasons (Chapter III).

Table 1. Types and numbers of samples used in the chapters of this thesis.

Type of samples	Origin of samples	Chapter I	Chapter II	Chapter III
Tornio-Kalix juveniles	Tornio and Kalix	n = 749	n = 361 ^d	n = 243 ^a , n = 361 ^b
Smolt samples from 2011	Tornio	n = 196 ^b		
Adult catch samples from 2009-2010	Tornio	n = 287 ^c		
Baseline samples from other stocks	Wild: Råne, Simo, and Vindel Rivers, reared: Ii, Kymi, Lule, Oulu, Simo and Tornio stocks			n = 175 ^a , n = 313 ^b
Adult catch samples from 1928-2020	Tornio and Kalix			n = 2,745

^a Used for SNP panel development, ^b used for GSI.

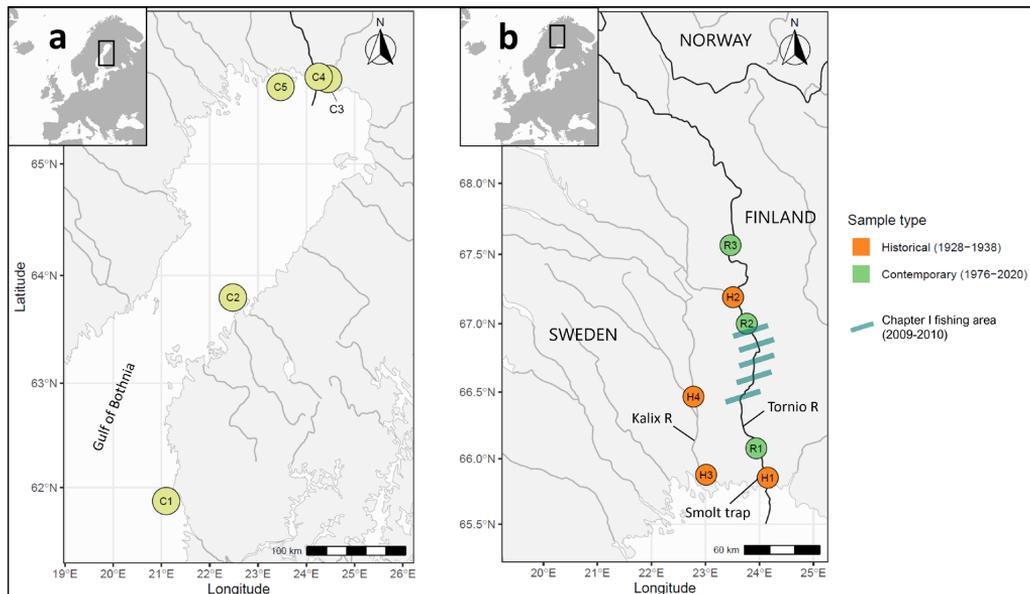


Figure 4. Coastal and river sampling of Atlantic salmon adult and smolt catches (Chapters I-III), showing sampling areas from **a** the coast of Gulf of Bothnia (years 2019-2020), and **b** from the Tornio and Kalix Rivers (years 1928-2020). Coded fishing areas on the map: C1 = Merikarvia, C2 = Luoto, C3 = Kemi River mouth, C4 = Tornio River mouth, C5 = Coastal fishing area in Sweden, R1 = Tornio River Downstream area, R2 = Pello-Lappea, R3 = Kihlanki, H1 = Kiviranta, H2 = Kengisfors, H3 = Kalix River Downstream area, H4 = Rödupp. The darker lines depict national borders, including the Tornio River that flows on the border of Finland and Sweden.

3.2 Genetic markers

First, we applied 18 microsatellite markers to samples of salmon from different life stages, to investigate the genetic population structure within the Tornio and Kalix Rivers, and to examine its associations with variation in freshwater and marine life-history traits (Chapter I).

Second, we used a genome-wide SNP (single nucleotide polymorphism) array of 60,252 markers developed for Atlantic salmon (CIGENE, Norwegian University of Life Sciences, Norway) to explore the fine-scale population genetic structure of the Tornio-Kalix salmon in more detail (Chapter II), along with examining broader genetic

structure among other northern Baltic salmon stocks in the genetic baseline (Chapter III). Moreover, we used the SNP array to identify genomic signatures of fine-scale local selection in the Tornio-Kalix stock (Chapter II).

Third, we used a genotyping-in-thousands by sequencing approach (GT-Seq; Campbell *et al.* 2015) to genotype 229 SNPs for genetic stock identification (GSI) and monitoring of life-history loci in coastal and river catches of Baltic salmon collected between 1928 and 2020 (Chapter III). The outline for designing and using the panel is described below.

3.2.1 SNP panel development and use for genotyping of wild catch samples

We applied information from the first two studies to design and develop a GT-seq SNP marker panel for investigating whether coastal and river fishing of wild Baltic salmon target specific genetic subpopulations and life-history loci over the fishing seasons (Chapter III). Making use of SNP markers allowed monitoring of specific adaptive loci, and higher precision of GSI than with the microsatellites used in Chapter I. This collection of markers targeted 229 SNPs, of which in total 169 passed our quality control thresholds.

The workflow for the development and use of the SNP panel is outlined in Figure 5 and described in detail in Chapter III. Figure 5 also describes the types and numbers of samples used in the SNP panel development, and its application in GSI and monitoring of adaptive loci (Chapter III). It should be noted that while we were developing the SNP panel, a part of the genotyping data for the final baseline were still being generated. Thus, a preliminary baseline was used for the identification of SNPs to be used in the panel. Due to this, the panel did not contain some of the candidate SNPs detected with the full Tornio-Kalix baseline in Chapter II. Nevertheless, the panel included well-known adaptive loci, which allowed us to address whether the timing of fishing could alter life-history diversity of the studied Baltic salmon stocks.

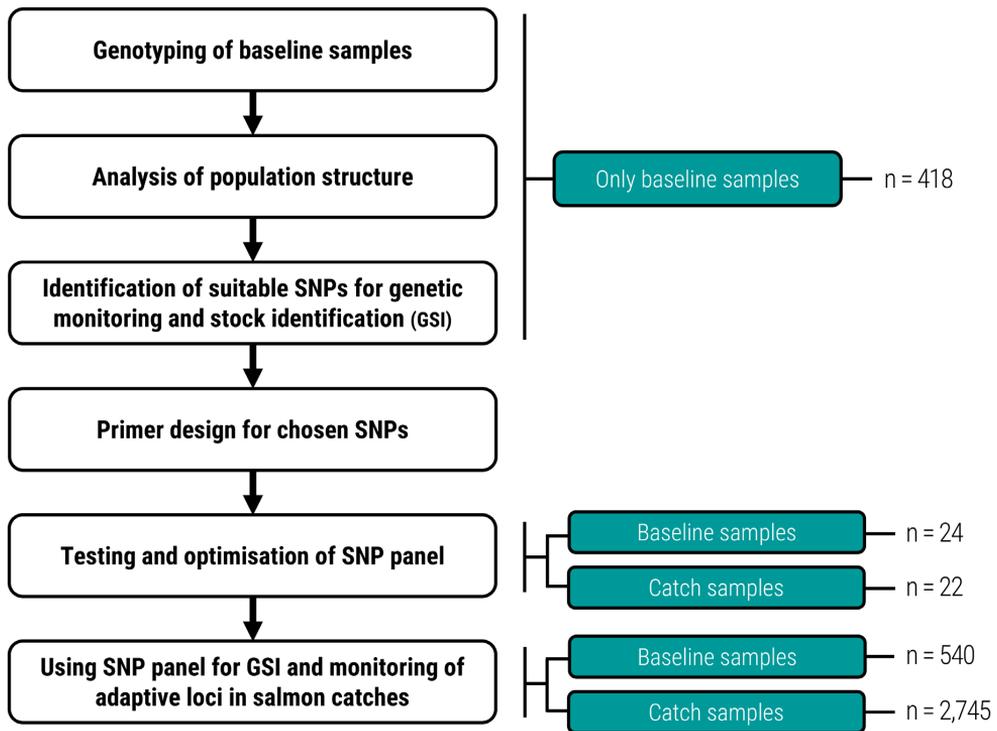


Figure 5. Diagram describing the design and development of the genotyping-by-sequencing SNP panel and the subsequent genetic stock identification (GSI) and monitoring performed with it (Chapter III). *n* refers to the numbers of samples used at each step.

3.3 Detection of candidate adaptive loci

We used a combination of “outlier” approaches, univariate and multivariate genotype-environment association (GEA) analyses, and XP-EHH tests to search for genomic regions exhibiting signals of divergent selection (Chapter II) (summarised in Table 2) in the Tornio-Kalix salmon stock. We used these genome scans to identify SNP markers exhibiting exceptionally i) high allelic variation among sampling sites (outlier analyses), ii) strong associations with environmental parameters (GEA analyses), or iii) low genetic variation surrounding them (i.e. regions exhibiting elevated haplotype homozygosity). The aim of this was to improve our understanding of adaptive genetic diversity and its potential drivers in this wild salmon stock.

To summarise the principle of the different methods used in Chapter II, first, outlier analyses attempt to identify signatures of selection by comparing among-population allelic variation to an estimated neutral distribution of genetic variation. Second, the haplotype-based summary statistic (XP-EHH test) compares extended haplotype homozygosity (EHH) among populations to detect signals of population-specific selective sweeps, characterised by long haplotypes at high frequency and low genetic diversity near adaptive alleles (Szpiech 2022). Finally, GEA analyses search for selection signatures by identifying strong correlations between genetic and environmental variation. Whereas univariate GEA analyses test one locus and

environmental predictor at a time, multivariate GEA analyse multiple loci and predictors simultaneously. The multivariate method, such as a redundancy analysis (RDA), may be better suited to detect weak, multilocus signals of selection (Forester *et al.* 2018).

Only a subset of the environmental variables available for the Tornio-Kalix system were used in Chapter II, due to many of them being highly correlated with each other. In particular, distance from river mouth, elevation, latitude and mean annual temperature are strongly correlated in the Tornio-Kalix, and therefore only one of these predictors (distance from river mouth) was retained. However, this predictor can be assumed to reflect some variation in the other above-mentioned variables, which is important to note in the interpretation of the associations from our GEA analyses.

Following Pritchard *et al.* (2018) and Zueva *et al.* (2021), we considered the top-ranked 0.5% SNPs from each test as candidate outliers. The reasoning for this was based on the different methods we used having different ways of estimating neutral variation that they use as a reference for identifying outlying genetic variation. The model-based approaches assume that signals of selection reflect demographic history, but a realistic demographic model is difficult to fit. Thus, we used an approach of consistently considering the top-ranked 0.5% SNPs of the empirical distribution from the different tests. When selection is indeed acting on loci in a dataset, this approach can be powerful in detecting important genomic regions (reviewed in Hahn 2019).

A particular caveat in genome scans with large datasets is the risk of false positives due to multiple testing (reviewed in Hahn 2019). To mitigate this, we considered only overlapping results from the independent tests by the different approaches. To further evaluate the validity of our candidate genomic regions, we searched the literature for their potential functional relevance in salmonids and other fish. This was also useful for assessing potential repeatability of the signals across different evolutionary lineages.

Table 2. Methods and their test statistics used to detect signals of local selection in Chapter II.

Approach	Software	Test statistic	Method description	Definition of candidate SNPs*
Genome scans for outliers	<i>pcadapt 4.3.2</i> (Privé <i>et al.</i> 2020)	Mahalanobis distances, p-value	Ordination method that identifies outliers based on correlations between genetic markers and population structure determined by the optimal number of principal components.	“Outlier-based candidates” were SNPs in the top-ranked 0.5% in all of the tests.
	<i>BayPass 2.31</i> (Gautier 2015)	Absolute XtX	Identifies outliers by estimating per-SNP deviations from the underlying genome-wide population structure based on a neutral covariance matrix of population allele frequencies.	
	<i>BayeScEnv v1.1</i> (de Villemereuil and Gaggiotti 2015)	q-value, alpha parameter	Bayesian model-based method that estimates the posterior probability that a given locus is under selection.	
Univariate genotype-environment association (GEA)	<i>LFMM 2</i> (Caye <i>et al.</i> 2019)	q-value	Model-based method that detects outliers by evaluating associations of allele frequencies with environmental variables while using latent factors to account for population structure.	“Univariate GEA candidates” for each environmental variable were SNPs in the top-ranked 0.5% in all of the tests.
	<i>BayPass 2.31</i>	Absolute Pearson correlation coefficient (r)	Identifies loci associated with population-specific environmental covariates, while accounting for underlying genome-wide population structure as above.	
	<i>BayeScEnv v1.1</i>	g, q-value	Bayesian model-based method that identifies outlier loci showing an increase in between-population F_{ST} with increasing environmental differentiation, while assuming the populations are independent.	
Multivariate GEA (redundancy analysis; RDA)	<i>vegan 2.6-4</i> (Oksanen <i>et al.</i> , 2022)	Loadings in the ordination space	Ordination-based method that determines how sets of loci covary in response to the multivariate environment, and can detect relatively weak, multilocus signatures of selection (Forester <i>et al.</i> , 2018). Partial RDA can be used to correct for population structure.	“RDA candidates” had extreme loadings on the RDA axes.
Haplotype-based	<i>selscan v1.3.0</i> (Szpiech and Hernandez 2014)	XP-EHH (maximum absolute normalised score)	Identifies genomic regions suggestive of selective sweeps, indicated by elevated haplotype homozygosity.	“XP-EHH candidates” were in SNPs the top-ranked 0.5%.

* In Chapter II.

4. RESULTS AND DISCUSSION

4.1 Upstream-downstream genetic divergence is linked to life-history variation

In Chapters I and II, we found substantial genetic differentiation within the large Tornio and Kalix Rivers: Atlantic salmon from the upper reaches differed genetically from individuals from the lower reaches, regardless of river system. Using SNP markers on a dataset that included additional sampling sites to those used in Chapter I, we identified in total four genetic clusters in the river system (“lower” and “upper Tornio-Kalix”, “upper Lainio” tributary, and “Ängesån” tributary) (Chapter II; Figure 6).

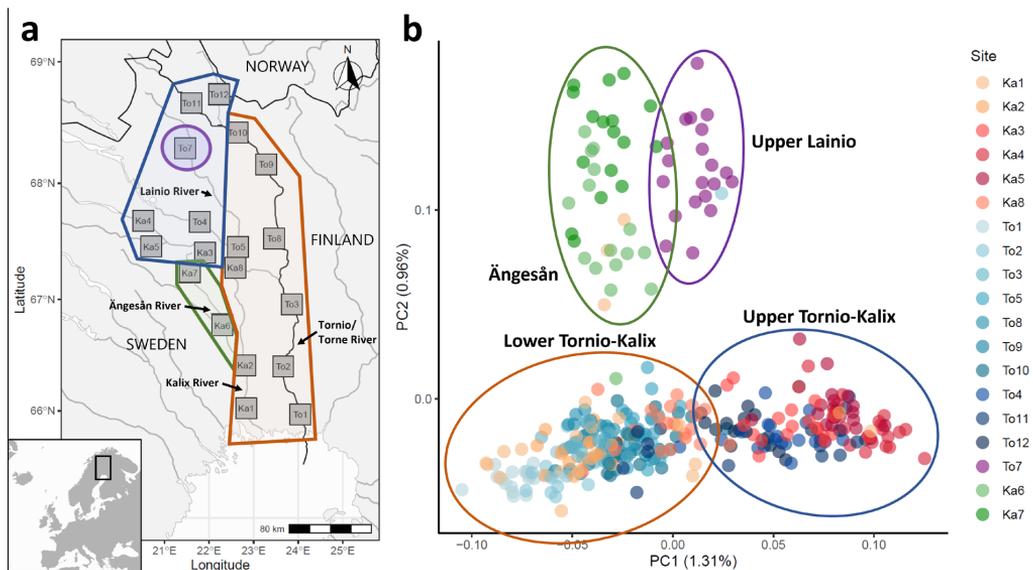


Figure 6. **a** A map of the Tornio-Kalix River system, with the identified genetic subpopulations overlaid on it, and **b** a principal component analysis (PCA) visualising the genetic population structure of the Tornio-Kalix salmon stock, showing the first two PC axes. The proportion of variance explained by each principal component is indicated on the axis labels. Each point represents an individual, and their distribution on the axes depicts their genetic distance from each other. The paler coloured points correspond to individuals from sites closer to the river mouths. The PCA was run using an LD-pruned dataset of 20,745 SNPs.

Overall, the population structuring within the Tornio-Kalix system was significant but relatively shallow (global $F_{ST} = 0.015$; Chapters I and II). This genetic differentiation was associated with an underlying pattern of isolation by distance (IBD). This common phenomenon in nature means that the genetic divergence between individuals was positively correlated with their geographic distance (Jenkins *et al.* 2010; Meirmans 2012), indicating higher gene flow between neighbouring than distant sites, or past population expansion (Slatkin 1993). Additionally, we observed rather high genetic homogeneity between the Tornio and Kalix Rivers, some of which could possibly be explained by the bifurcation connecting them. Compared to other large salmon rivers, this pattern and level of substructuring in the system resembles for example the

Varzuga (in Russia) and Miramichi (in Canada) Rivers (Primmer *et al.* 2006; Wellband *et al.* 2018), but is in stark contrast to the geographically close and physically similar Tenö (Deatnu in Northern Sámi, Tana in Norwegian) River that hosts almost 30 genetically distinct Atlantic salmon subpopulations (Vähä *et al.* 2017). This comparison underlines that population genetic differentiation of Atlantic salmon at fine spatial scales varies across geographic regions (Dionne *et al.* 2009).

The genome-wide SNP array allowed higher power than the microsatellites to identify population substructuring in clustering methods (Chapters I and II). However, the SNPs and microsatellites found a similar pattern of population genetic divergence between the upper and lower river areas, which was also in line with studies from this river system using a limited number of allozyme markers and restricted geographic coverage (Ståhl 1981, 1983; Jansson 1993). This may indicate temporal stability of the population structure, and suggests that a relatively low number of more traditional markers, such as microsatellites, can be sufficient in characterising large-scale neutral population structuring.

Compared to the lower Tornio-Kalix, genetic diversity was slightly reduced in the upper genetic cluster and in the Ängesån and upper Lainio tributaries. This pattern was consistent across most of the diversity metrics evaluated for the microsatellites and SNPs, such as allelic richness, heterozygosity or runs of homozygosity (ROH) (Chapters I and II). This might suggest that the upstream subpopulations have experienced stronger bottlenecks and genetic drift and have lower effective population sizes (N_e). These results are concordant with observations and general predictions across a range of taxa that neutral genetic diversity is higher in downstream parts of riverscapes (Raeymaekers *et al.* 2008; Paz-Vinas *et al.* 2015; Blanchet *et al.* 2020).

Studying smolts migrating from the Tornio River to the sea, we found that smolts from the upper river reaches were older and tended to reach the river mouth later in the season than their downstream-origin counterparts (Chapter I). We also found an association between the genetic structure and seasonal migration timing of adults returning from the sea to spawn (Chapters I and III). Inferred from catch dates (a good proxy for migration timing), adults originating from the upper river reaches migrated earlier in the sea (Chapter III) and returned to the Tornio River earlier in the season than adults from the lower reaches (Chapters I and III). Notably, salmon from the upper Lainio were particularly old (in terms of their sea age; Chapter III) and frequent in the early season catches (Chapter III). These results highlight the potential impact of seasonal fishing timing on the different subpopulations. The results of Chapters II and III shed light on the potential genetic basis of these spawning migration differences, how fishing targets adaptive genetic variation associated with this variation, and what the evolutionary implications of that might be.

4.2 Signatures of local selection on adaptively relevant loci

A combination of GEA analyses and outlier- and haplotype-based approaches revealed strong candidates for genomic regions exhibiting signatures of fine-scale local selection in the Tornio-Kalix salmon stock (Chapter II). Many of the candidate genome regions (haploblocks) contained loci of ecological relevance, including genes previously documented to be associated with variation in key life-history traits of Atlantic salmon,

such as in the timing of maturation or migration (*six6*, *taar13c-like*; Barson *et al.* 2015; Pritchard *et al.* 2018; Sinclair-Waters *et al.* 2022), or feeding and appetite control (*pomca*, *mc4r*; Kalanathan *et al.* 2020, 2023; Norland *et al.* 2023). Furthermore, many of the candidate haploblocks contained genes possibly involved with local adaptation to environmental conditions in salmonids or other fishes, supporting their putatively adaptive role in the Tornio-Kalix stock. Overall, these results shed light on the role of genomic variation in potential local adaptation of this relatively weakly subdivided salmon stock. Moreover, this work provided support for the repeatability of selection signatures across broad geographical areas and evolutionary lineages.

We observed genotype-environment associations in all candidate haploblocks, suggesting that variation in the river environment may play a role in adaptive differentiation of Tornio-Kalix salmon. For instance, precipitation variation was often associated with allelic variation of SNPs in our candidate haploblocks and is therefore a candidate environmental driver of local adaptation (Bourret *et al.* 2013a; Hecht *et al.* 2015). The functional relevance of the detected candidate loci could also be related to local selective pressures from, for example, elevation (Rougemont *et al.* 2023), water chemistry (Bourret *et al.* 2013a), temperature (Dionne *et al.* 2008) or photoperiod (Garcia De Leaniz *et al.* 2007). However, as anadromous salmon encounter widely varying freshwater and marine environments during their life, interpreting the possible adaptive role of candidate genes in specific environments is challenging. Therefore, without experimental manipulations the genotype-environment associations provide only indications of possible drivers of local adaptation and should be interpreted with caution (e.g. Pavlidis *et al.* 2012; Bekkevold *et al.* 2020). Nevertheless, improved knowledge of potential environmental drivers of population structuring and local adaptation may allow predicting future evolutionary trajectories of salmon stocks and identifying particularly vulnerable populations under different scenarios of environmental change (Capblancq *et al.* 2020; Capblancq and Forester 2021; Layton *et al.* 2021).

In general, the allele frequencies of many candidate SNPs closest to adaptively relevant genes in the candidate haploblocks reflected the main upstream-downstream genetic divergence in the Tornio-Kalix system (Figure 7 shows allele frequency variation of SNPs closest to four candidate genes discussed here). Similar patterns of concordant allelic variation at adaptive and neutral markers have been observed in other salmonid lineages (Moore *et al.* 2014; Xuereb *et al.* 2022). This pattern could possibly reflect a strong underlying influence of local adaptation on population structuring in the system (Moore *et al.* 2014). Overall, differential selective pressures experienced by salmon from different parts of the river system could underlie the general pattern of spatial variation in the candidate SNPs' allele frequencies.

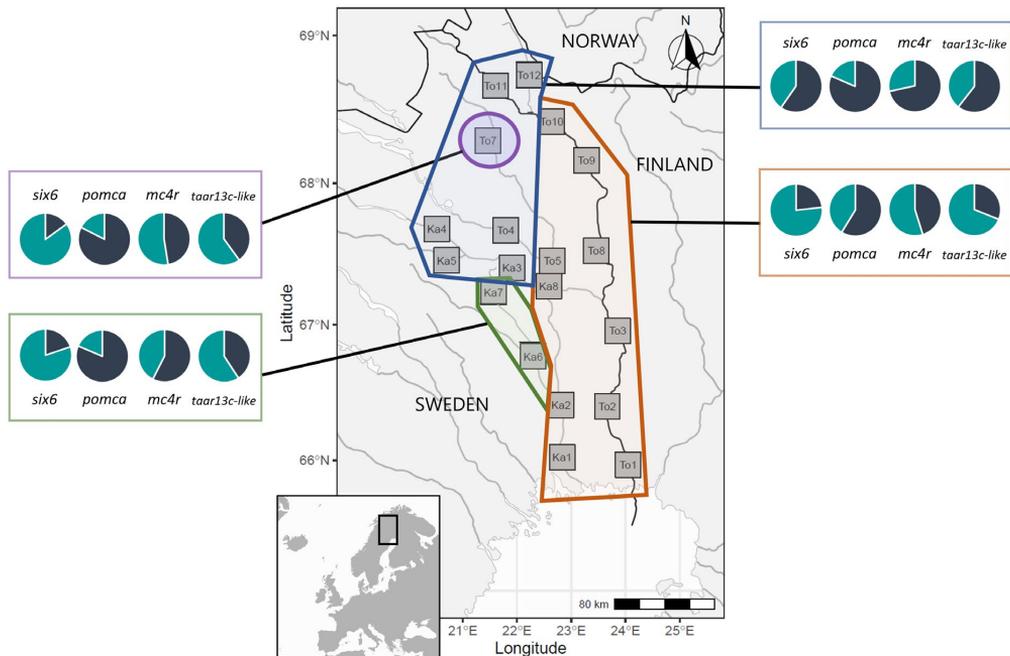


Figure 7. Allele frequencies of the physically closest candidate SNPs to four candidate genes discussed here (*six6* and *pomca* on chromosome 9, *mc4r* on chromosome 14, *taar13c-like* on chromosome 21) (Chapter II). The pie charts show the mean allele frequencies of the SNPs, combined over the different sites in the four genetic subpopulations identified in Chapter II (lower and upper Tornio-Kalix, upper Lainio, Ångesån). The two colours per SNP correspond to their different alleles.

The candidate haploblock that contained the highest number of candidate genes and was identified by all analysis methods included the *six6* gene (Figure 8). Although our data cannot ascertain that *six6* is the target of selection in this genomic region, it is known to be involved in fine- and broad-scale local adaptation and/or spatial differentiation in salmonids (Pritchard *et al.* 2018; Zueva *et al.* 2021; Gabián *et al.* 2022; Tigano and Russello 2022; Andrews *et al.* 2023). It is also associated with age at maturity in Atlantic salmon and Pacific salmonids (Barson *et al.* 2015; Sinclair-Waters *et al.* 2020, 2022; Willis *et al.* 2020; Waters *et al.* 2021; Jensen *et al.* 2022a; Kess *et al.* 2022; Besnier *et al.* 2023). However, *six6* may be associated with some other trait that is correlated with age at maturity, in a population-specific way (e.g. migration timing; Pritchard *et al.* 2018; Wellband *et al.* 2018; Zueva *et al.* 2021; Kess *et al.* 2022). It may also have multiple adaptive roles, some of which might be life stage-specific (Aykanat *et al.* 2020). In Chapter III, we confirmed that *six6* affected both age at maturity and catch date (indicating spawning migration timing) of wild Baltic salmon. Therefore, this thesis adds to the growing knowledge of the effects of *six6* on adaptively important variation in natural populations and suggests a level of genomic parallelism underlying putative local adaptation over the global range of salmonids (e.g. Zueva *et al.* 2021).

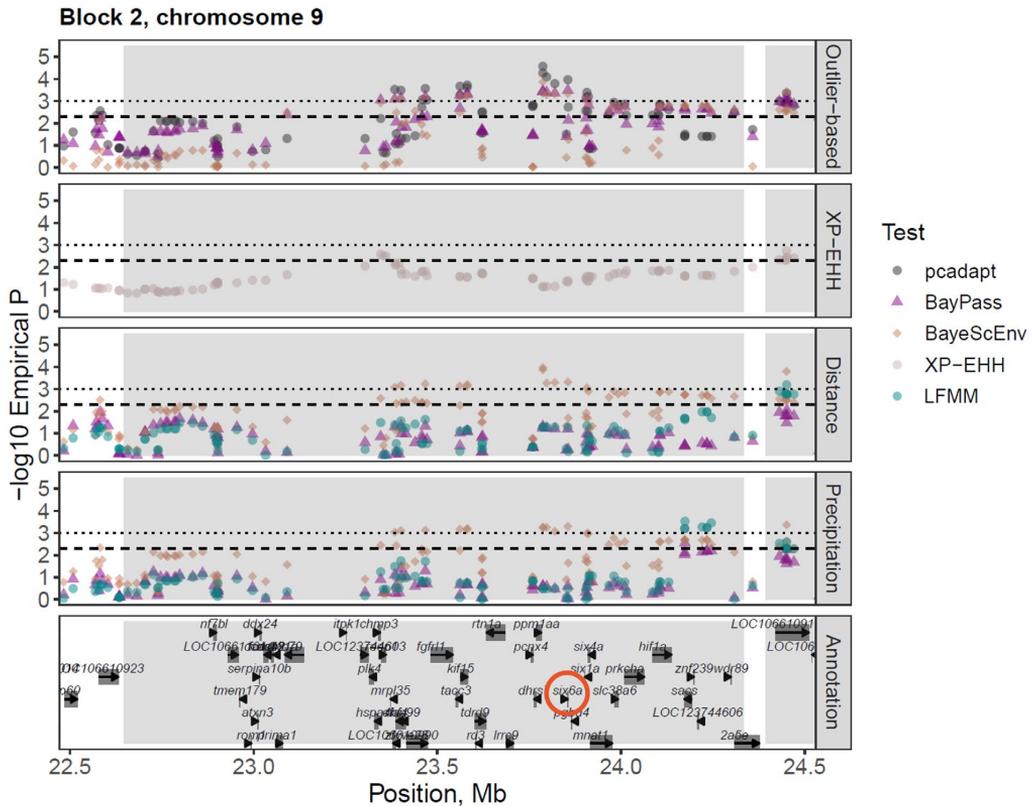


Figure 8. Signatures of local selection on the candidate haploblock with the highest number of candidate SNPs and genes in Chapter II. This block contained the *six6* gene (circled in red). The dashed and dotted lines indicate empirical $p < 0.005$ and $p < 0.001$, respectively (empirical $p = \text{SNP rank} / \text{total number of tests}$). The grey rectangles show the boundaries of candidate haploblocks identified in Chapter II. The panels from top to bottom show empirical p -values for outlier-based tests, XP-EHH test, univariate GEA analyses of distance from river mouth (also a proxy for e.g. temperature-related variation) and of the environmental variable (annual precipitation, i.e. BIO12) associated with candidate SNPs in the haploblock in both univariate and multivariate GEA analyses.

4.3 Temporally varying selection pressures on adaptive loci imply potential for human-induced evolutionary change

Knowledge of the genetic basis of age at maturity in Atlantic salmon, combined with genotyping catch samples from the northern Baltic Sea collected throughout fishing seasons, provided us with a rare opportunity to infer possible evolutionary impacts of harvesting on wild populations (Chapter III). First, we confirmed that the known large-effect loci *vgll3* and *six6* affected age at maturity in the studied Baltic salmon catches. Then, we discovered that fishing in the early season preferentially targeted the *vgll3**L variant strongly linked to older age at maturity (Figure 9; Chapter III). This within-season pattern was consistent across years, suggesting that strong fishing in the early season could lead to a reduction in the mean reproductive age and size of Baltic salmon. The potential for this kind of an evolutionary effect resulting from early-season fishing of Atlantic salmon has been suggested previously (Consuegra *et al.* 2005; Quinn *et al.* 2006). The results from this thesis improve our understanding of the potential

mechanisms that are behind seasonal fishing timing possibly causing evolutionary changes in Atlantic salmon age at maturity.

Genetic monitoring of the wild salmon catches allowed us to examine migration patterns that are difficult to study in laboratory conditions (Elmer 2016). We found both *vgll3* and *six6* to affect return migration timing, regardless of sea age that is known to be negatively correlated with the timing of spawning migration. This adds to our understanding of the genetic basis of migratory diversity, and has management implications for Baltic salmon (see below).

Finally, by retrospectively monitoring temporal genetic changes in the adaptive loci, we found that their allele frequencies in the Tornio River catches have changed substantially during the last century. The long-term *vgll3* allele frequency fluctuations were more pronounced than those of *six6* and largely followed known age structure changes in the Tornio catches over time. This further suggests that possible future reductions in the *vgll3**L frequency are likely to lead to corresponding reductions in the mean age at maturity of Tornio-Kalix salmon.

To summarise, we found temporal variation in how fishing targets large-effect loci, thus creating potential for human-induced evolution in age at maturity of wild salmon populations. Overall, this study provides a concrete example of using genomic approaches to infer anthropogenic impacts on adaptively important genetic variation in nature.

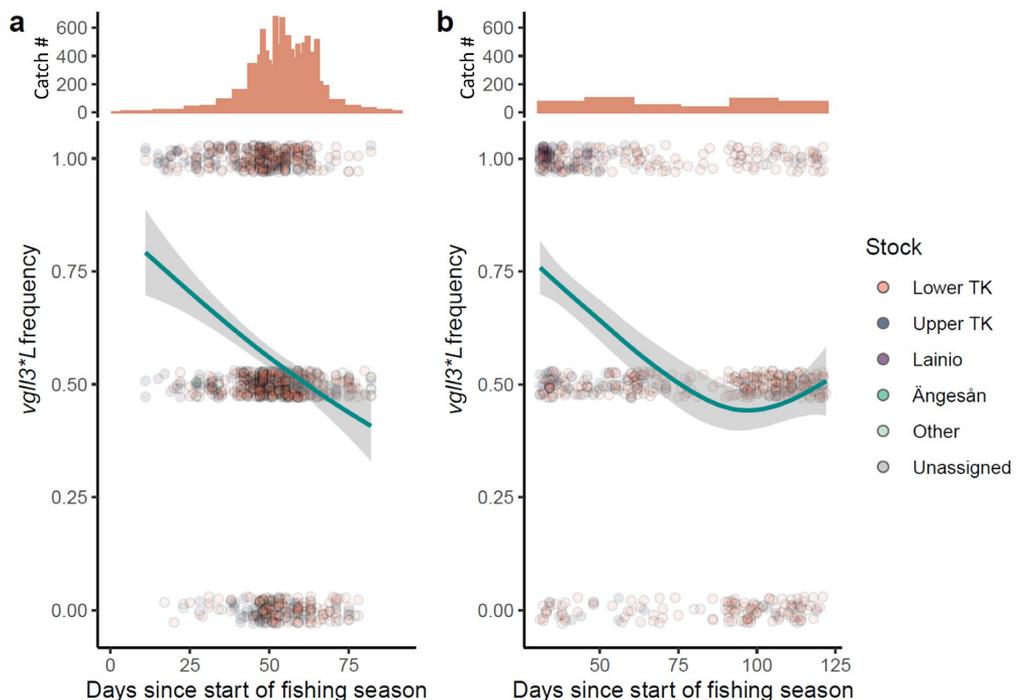


Figure 9. *vgll3**L (associated with older age at maturity) allele frequency in **a** coastal wild salmon catches and **b** Tornio River catches during 2019-2020. The lines depict a relationship between *vgll3**L and catch date, fitted with a GAM, whereas the grey area around the lines illustrates the uncertainty of the fitted relationship (95% confidence intervals). The histograms above show the

estimated daily catch sizes (number of salmon caught per day) in these areas for the duration of the fishing season. The data points represent the *vgll3* genotype and assigned origin of individual samples. The points are jittered on the y-axis to aid figure interpretation.

4.4 Conservation and management implications

This thesis provides recommendations for conservation and management of wild Atlantic salmon populations in the northern Baltic Sea region. The results of this research are actively communicated to decision-makers of Baltic salmon fisheries management (e.g. (Palm *et al.* 2023) and have high potential for being useful in improving the long-term sustainability of wild Baltic salmon fisheries.

As each year spent at sea before reaching maturation increases the body size of Atlantic salmon substantially, age at maturity is a highly relevant trait for fisheries management. Chapter III demonstrated that seasonal fishing timing can be a potential selective force that may cause changes in this trait in Baltic salmon. Genetic monitoring of fisheries catches provided a simple take-home message: intensive early-season fishing may reduce the proportion of *vgll3**L alleles in the spawning stock, and consequently lead to a reduction in mean age at maturity of Tornio-Kalix salmon. Interestingly, the frequency of *vgll3**L was high in early-season catches even independent of sea age. This indicates that by selecting against *vgll3**L, strong early-season fishing has the potential to cause evolutionary changes towards younger maturation age in salmon, even if older age classes would be left unharvested (e.g. in case of an upper size limit). These results underline that temporal regulation of fisheries plays a central role in preserving salmon life-history diversity (Saura *et al.* 2010; Mobley *et al.* 2021). Our results thus support the notion that restrictions on early-season fishing are important for maintaining a healthy proportion of older spawners in northern Baltic salmon stocks.

Genetic variation in life-history loci such as *vgll3* and *six6* maintains a portfolio of maturation and migration phenotypes in salmon stocks. Within-river phenotypic differentiation in the Tornio-Kalix appeared to be at least partly driven by genetic variation at these loci (Chapter III). Preserving this diversity by avoiding harvest-induced selection can promote the populations' resilience to climate change (Kovach *et al.* 2015), help them endure stochastic environments and reduce temporal variability in the numbers of individuals that can be sustainably harvested from the stock (Schindler *et al.* 2010). This type of phenotypic diversity can in turn be important for the functioning of whole species communities and ecosystems (Hughes *et al.* 2008; Des Roches *et al.* 2018). Safeguarding this intraspecific variation should be the aim of salmon management (Jacobson *et al.* 2020), and to do so the potential evolutionary outcomes of temporally varying fishing mortality need to be carefully considered in regulating fisheries. In a broader context, to meet international objectives for biodiversity conservation and sustainable development, evolutionary principles must be integrated into policies much better than they currently are (Carroll *et al.* 2014). To this end, this thesis provides relevant insights for a better understanding of how fisheries policy may influence specific aspects of intraspecific diversity.

Chapters I and III demonstrated that harvest timing during the season influences how fishing targets the specific Tornio-Kalix subpopulations: early-season catches contained higher proportions of salmon originating from upstream river reaches than

catches in the later season. The upstream subpopulations may be more vulnerable to the impacts of fisheries exploitation, mainly due to their longer life cycle and migrations compared to downstream-spawners (Chapters I and III). They may also face higher fishing mortality relative to their population size. This notion is based on our GSI analysis from Chapter I that found a higher proportion of upstream-origin individuals in adult than smolt catches. However, as the smolt dataset contained only one year, this evidence is not conclusive. Detailed knowledge of the different subpopulation sizes in the Tornio-Kalix system would allow evaluating the proportional harvesting pressures faced by salmon spawning in different parts of the system. Future investigations of stock proportions of smolts from multiple years, as well as studies of effective population sizes could shed light on this issue. Regardless of the exact harvesting pressures, this work showed that seasonal fishing timing is important to consider in order to minimise the risk of overexploiting the upstream subpopulations.

Identifying potentially adaptive loci is the first step in developing genetic assays that can be used in monitoring and guiding management strategies to help preserve variation at these loci (Hohenlohe *et al.* 2021). In addition to the known life-history loci such as *vgl3* and *six6*, other, putatively adaptive genetic variation identified in Chapter II could possibly be used for monitoring adaptive responses to natural or anthropogenic influences, and for example be used as indicators for climate change responses (see Kovach *et al.* 2012). However, the strategy for preserving adaptive diversity should generally not be based on single loci – especially if the link between the putatively adaptive genetic variation and a phenotype has not been validated (Kardos and Shafer 2018).

Finally, we also examined the broader population structure among the different northern Baltic salmon stocks that have not been studied with this resolution of genetic markers before (Chapter III). As the Tornio River hatchery broodstock and wild salmon from the lower part of the river system were genetically alike, distinguishing them with GSI appears to be very difficult. Furthermore, the population structure analyses indicated interesting, reasonably strong genetic resemblance between the Oulu and Lule River broodstocks. These two rivers are not very close to each other geographically (they have their mouths on the opposite sides of the Bothnian Bay, c. 165 km apart), but their broodstocks share some ancestry that likely explains the relatively strong genetic resemblance between the two stocks: salmon from Indalsälven, Skellefteälven and Umeälven were used in creating both broodstocks (Säisä *et al.* 2003; Vasemägi *et al.* 2005). Overall, the SNP panel developed in Chapter III can be a useful tool for future studies of these Baltic salmon broodstocks and wild populations. This study therefore improved the tools available for identifying different Baltic salmon stock components from mixed-stock fishery catches, and for quantifying selective pressures and harvesting mortality imposed on the stocks by fisheries.

5. CONSIDERATIONS AND FUTURE DIRECTIONS

5.1 Genomic basis of local adaptation

The genome scan approaches used in Chapter II are efficient in detecting strong signals of directional selection. Our rather conservative approach of accounting only for candidate genomic regions identified by multiple software and multiple types of analyses strengthens the validity of the discussed loci. However, it is likely that this approach missed loci under weaker selection (Whitlock and Lotterhos 2015), which may mean that the total number of genes involved in local adaptation in the Tornio-Kalix system is much higher (Konijnendijk *et al.* 2015). In addition, the density of the SNP array used in this thesis is not very high and likely does not cover all adaptively relevant genomic regions. Nevertheless, our approach identified many loci with previously suggested adaptive relevance in salmonids and more broadly in fishes, supporting their role as true candidates involved in local adaptation.

A challenge in interpreting genome scans is that footprints of divergent selection can be confounded with genetic patterns generated by neutral, demographic processes, such as genetic drift (Gautier 2015). Furthermore, inferring the potential drivers of putatively adaptive genetic variation is particularly complicated when the drivers of selection are collinear with population structure. In the Tornio-Kalix River complex, certain climatic predictors (e.g. temperature) and population genetic structure are strongly correlated along the north-south gradient, the drivers of selection signatures in this system difficult to distinguish (Excoffier *et al.* 2009; Wang and Bradburd 2014). In addition, environmental predictors not included in our GEA analyses, but correlated with some of the retained variables mean that genetic variation associated with distance from river mouth, for instance, may reflect an association with elevation or temperature (Chapter II). Furthermore, some of the candidate regions identified could be related to gene regulation. Therefore, complementary analyses and experimental manipulations are required to understand how the candidate loci may be involved in local adaptation.

Lastly, this thesis did not focus on chromosomal rearrangements that are increasingly recognised as important in local adaptation (Cayuela *et al.* 2020; Han *et al.* 2020; Le Moan *et al.* 2021; Hoikkala and Poikela 2022; Fuentes-Pardo *et al.* 2023). Their possible adaptive role in Baltic salmon should be an avenue of future research.

5.2 Management-related perspectives

This thesis provided evidence for spatiotemporal variation in fishing pressures to potentially impact salmon life-history diversity. On the other hand, the evolutionary responses of Atlantic salmon to selective fishing can be complicated to predict and depend on the genetic architecture underlying age at maturity (Kuparinen and Hutchings 2017; Oomen *et al.* 2020).

Our data allowed us to only speculate about the factors behind the observed long-term fluctuations in *vgll3**L frequencies in the Tornio-Kalix catches (Chapter III). In addition, due to the long generation time (typically six or more years) of northern Baltic

salmon, we could not observe or infer potential evolutionary impacts of the fishing regulation change since 2017 with our dataset ending in 2020. This means that the potential evolutionary outcomes of the currently allowed “advanced early-season coastal fishing” on Baltic salmon stocks remains an important question for future research to address.

Finally, our results suggest possible local adaptation to climatic conditions in the Baltic salmon subpopulations, which will be increasingly relevant for future management considerations under intensifying climate change. Arctic ecosystems and fresh waters have been called “harbingers of ecological change” (Heino *et al.* 2020) as they are warming up faster than more southern areas (Prowse *et al.* 2006). This highlights a need to monitor and understand future responses of populations to environmental changes in these ecosystems (Alioravainen *et al.* 2023). To help with this, candidate loci identified by the GEA analyses (Chapter II) could offer a rough basis for predicting responses and evolutionary trajectories of Tornio-Kalix salmon to rapidly changing conditions.

6. CONCLUSIONS

This thesis demonstrated that the population genetic structure of the largest wild Baltic salmon stock is linked with life-history differences that are associated with genetic variation at large-effect loci. This work also showed that these ecologically important loci face spatially and temporally varying selection pressures from commercial and recreational fisheries. This indicates that anthropogenic, temporally varying selection on these loci has the potential to cause evolutionary changes in salmon life-history diversity. Figure 10 below illustrates a synthesising diagram of the results from this thesis.

The results from this thesis are actively communicated to decision-makers and can be used to guide the conservation and management of wild Atlantic salmon populations. To summarise, these results provide a tangible example of using genetic and genomic approaches to infer and monitor ecologically important genetic variation in nature and to guide management to mitigate human impacts on this diversity.

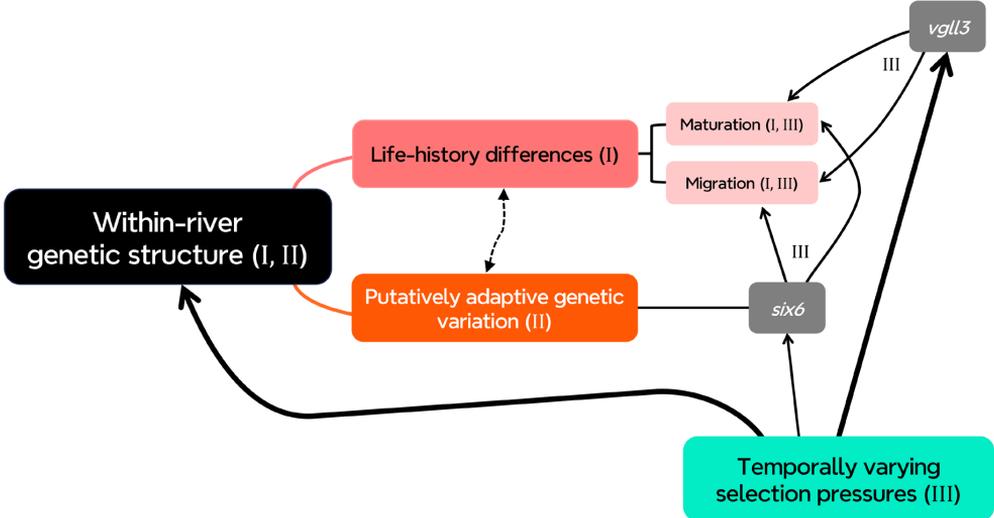


Figure 10. Synthesising diagram of the main results of the chapters in this thesis. The dashed arrow represents a putative connection between results, whereas the solid arrows illustrate strong evidence for connections found in this thesis. The Roman numerals refer to the thesis chapters.

ACKNOWLEDGEMENTS

Countless people have made my PhD journey possible and a pleasant experience. First, I'm grateful that I had the chance to work with and learn from two great supervisors. **Victoria (Vicky)**, your guidance and helpful, flexible attitude was essential, especially during the early days of my PhD work. Thank you for always encouraging me to explore different kinds of research avenues, and for being so resourceful about finding ways forward with any trouble that I would encounter. Also, thanks to you and your colleagues in Inverness for making me feel welcome during my visit there.

Craig, thank you for taking me into your group and providing the necessities for this research. As a supervisor, you always found time for me when I needed it. Maybe most importantly, you were often a voice of organisational reason and an endless source of admin-related pro-tips. I'm also thankful for the opportunities you gave me to present my work at conferences.

Atso, this project would not have been possible without you. I think with the amount of help and knowledge you offered, you could have easily been officially called my third supervisor. Whenever I would need anything, I could trust that you would deliver it quickly and in a much better format than I asked for. That was very comforting for me and invaluable for the project's success. I was also lucky to work with other helpful co-authors from Luke and SLU and benefit from their expertise (**Tapani, Ville, Stefan, Johan Ö, Johan D and Lo**). I also made fun and scientifically inspiring visits to Luke and SLU facilities.

Without naming single people, I wish to thank everyone involved with the material used in this project, all the way from the fishers and institutions collecting the salmon samples since the late 1920s, to people doing age measurements on the scales, and to those sending me environmental data, extracted DNA or any other type of material. I'm impressed that the century-old scale archives exist and humbled to have been able to use them.

This work also entirely depended on the funders who granted me with salary and other resources: thank you Societas pro Fauna et Flora Fennica, Kuopion Luonnon Ystäväin Yhdistys (Betty Väänänen rahasto), Raija ja Ossi Tuuliaisien säätiö, Suomen Luonnonsuojelun Säätiö, Alfred Kordelinin säätiö, Maa- ja metsätalousministeriö, Tornio River fishing license revenues, and the LUOVA doctoral programme.

My thesis committee members **Laura** and **Jaakko**, thanks for your thoughtful advice and interest in my work. Prof. **Jouni Aspi** and Assoc. Prof. **Jens Carlsson**, thank you both for your thorough and insightful pre-examination of this thesis. Prof. **Kathryn Elmer**, thank you for agreeing to be my opponent.

I was fortunate to work in the vast (extended) **EvolConGen** group. Thanks to all its past and present members, it has been really nice to know you and work with you. **Iikki** and **Morgane**, you deserve special credit for helping me in the lab during my busiest times. Iikki, thanks also for the Swedish translation of my abstract. **Ehsan**, thanks for being incredibly enthusiastic about gene functions and a unique person to talk to about life and baby fish. Former and current PhD students related to the group (**Marion, Andrew, Eirik, Paul, Katja, Xindi, Nora, Ossi, Dorian, Ksenia**), you deserve

an honorary mention for being such supportive peers and friends. Thesis tacos, skiing and skating, Hive and not-suffering-hiking trips took my mind off salmon when needed.

Everyone in **LUOVA**, thanks for the parties and other fun encounters. Special thanks go to the **LUOMUS floorball** gang for spectacular games every week.

Jack, better known as **Murkku-ukko**, thanks for the festivals, ventures and costly mushrooming trips we have experienced. Memories of them often make me smile – not once, twice but maybe even *thrice* a month. **Henry**, thanks for the good saunas and bad games. **Ronan**, thank you for your enthusiasm for all things natural and unnatural, and thanks for commenting on my thesis. **Carly**, your flag-drawing skills and good vibes are absolutely essential ingredients of fun times in Helsinki. **Joonas**, let's continue our refreshing businessman lunches where we discuss hot topics.

Lasselasse and **Miika**, we have hiked, paddled, played FIFA and squash, and listened to doom in the tuntsa – all of them priceless experiences without which life would be dry. Always nice to burst into some hörhiskely with you. The same applies to another Tsähkälän kahu (**Tino**), as well as to the other hiking crews with who we have conquered and not conquered wildernesses. Life in a warm office feels good after a bit of freezing in a sleeping sack. Thanks for teaching that, **Bone**.

Ville and Noora, or **Poika** and **Nopapoika**, thank you for being my Jyväskylä anchor. It was soothing to know that I could always come stay in “my room” and request endless beach volley and IMDB-point-optimised low-budget indie horror. I very much appreciated that. Related to you two, **KF**'s are always a blast. Out of them I would emerge with novel quirky memories to cherish. Thanks to everyone involved. Also, **Lampaat**, I'm happy to call you all friends.

To my family: I'm thankful for always having had an inspiring environment as a kid. I think the combination of a variety of books we had at home and being able to observe nature in the Harjunlampi pond drove me to become a biologist. I'm also very grateful for your support and encouragement during my PhD work. So, thank you, **Äiskä**, **Iskä**, **Ellu** and **Laura** and your families.

This research journey spanned a pandemic during which remote work would have been much less nice if we didn't share our home with two amazingly unique creatures. **Nipsu** and **Mörkö** distracted us and kept us constantly entertained with their purrs, quacks and shenanigans.

Finally, thank you **Emma**. Your constant support and understanding were invaluable during this process. I really appreciate your eagerness to celebrate any high points in my progress, and how you always listened to me and gave excellent advice during more difficult times. I am really lucky to have shared this phase in life with you.

REFERENCES

- Alioravainen N, Orell P, Erkinaro J (2023) Long-Term Trends in Freshwater and Marine Growth Patterns in Three Sub-Arctic Atlantic Salmon Populations. *Fishes* 8:441. <https://doi.org/10.3390/fishes8090441>
- Allendorf FW, Hard JJ (2009) Human-induced evolution caused by unnatural selection through harvest of wild animals. *Proc Natl Acad Sci U S A* 106 Suppl:9987–9994. <https://doi.org/10.1073/pnas.0901069106>
- Anderson LE, Lee ST (2013) Untangling the Recreational Value of Wild and Hatchery Salmon. *Mar Resour Econ* 28:175–197. <https://doi.org/10.5950/0738-1360-28.2.175>
- Andrews KR, Seaborn T, Egan JP, et al (2023) Whole genome resequencing identifies local adaptation associated with environmental variation for redband trout. *Mol Ecol* 32:800–818. <https://doi.org/10.1111/mec.16810>
- Autti O, Karjalainen TP (2012) The point of no return - Social dimensions of losing salmon in two northern rivers. *Nord Geogr Publ* 41:45–56
- Aykanat T, Rasmussen M, Ozerov M, et al (2020) Life-history genomic regions explain differences in Atlantic salmon marine diet specialization. *J Anim Ecol* 89:2677–2691. <https://doi.org/10.1111/1365-2656.13324>
- Ayllon F, Kjærner-Semb E, Furmanek T, et al (2015) The *vgl3* Locus Controls Age at Maturity in Wild and Domesticated Atlantic Salmon (*Salmo salar* L.) Males. *PLoS Genet* 11:1–15. <https://doi.org/10.1371/journal.pgen.1005628>
- Barson NJ, Aykanat T, Hindar K, et al (2015) Sex-dependent dominance at a single locus maintains variation in age at maturity in salmon. *Nature* 528:405–408. <https://doi.org/10.1038/nature16062>
- Bekkevold D, Höjesjö J, Nielsen EE, et al (2020) Northern European *Salmo trutta* (L.) populations are genetically divergent across geographical regions and environmental gradients. *Evol Appl* 13:400–416. <https://doi.org/10.1111/eva.12877>
- Benham PM, Bowie RCK (2023) Natural history collections as a resource for conservation genomics : Understanding the past to preserve the future. 367–384
- Besnier F, Skaala Ø, Wennevik V, et al (2023) Overruled by nature: A plastic response to environmental change disconnects a gene and its trait. *Mol Ecol* 1–12. <https://doi.org/10.1111/mec.16933>
- Blanchet S, Prunier JG, Paz-Vinas I, et al (2020) A river runs through it: The causes, consequences, and management of intraspecific diversity in river networks. *Evol Appl* 1–19. <https://doi.org/10.1111/eva.12941>
- Bourret V, Kent MP, Lien S, Bernatchez L (2013a) Landscape genomics in Atlantic salmon (*Salmo salar*): searching for gene-environment interactions driving local adaptation. *Evolution* 67:3469–3487. <https://doi.org/10.1111/evo.12139>
- Bourret V, Kent MP, Primmer CR, et al (2013b) SNP-array reveals genome-wide patterns of geographical and potential adaptive divergence across the natural range of Atlantic salmon (*Salmo salar*). *Mol Ecol* 22:532–551. <https://doi.org/10.1111/mec.12003>
- Butler DH, Koivisto S, Brumfeld V, Shahack-Gross R (2019) Early Evidence for Northern Salmonid Fisheries Discovered using Novel Mineral Proxies. *Sci Rep* 9:1–12. <https://doi.org/10.1038/s41598-018-36133-5>
- Campbell-Staton SC, Arnold BJ, Gonçalves D, et al (2021) Ivory poaching and the rapid evolution of tuskeness in African elephants. *Science* (80-) 374:483–487. <https://doi.org/10.1126/science.abe7389>

- Capblancq T, Fitzpatrick MC, Bay RA, et al (2020) Genomic Prediction of (Mal)Adaptation across Current and Future Climatic Landscapes. *Annu Rev Ecol Evol Syst* 51:245–269. <https://doi.org/10.1146/annurev-ecolsys-020720-042553>
- Capblancq T, Forester BR (2021) Redundancy analysis: A Swiss Army Knife for landscape genomics. *Methods Ecol Evol* 12:2298–2309. <https://doi.org/10.1111/2041-210X.13722>
- Carroll SP, Jørgensen PS, Kinnison MT, et al (2014) Applying evolutionary biology to address global challenges. *Science* (80-) 346:. <https://doi.org/10.1126/science.1245993>
- Carvalho PG, Satterthwaite WH, O'Farrell MR, et al (2023) Role of maturation and mortality in portfolio effects and climate resilience. *Can J Fish Aquat Sci* 80:924–941. <https://doi.org/10.1139/cjfas-2022-0171>
- Cauwelier E, Gilbey J, Sampayo J, et al (2018) Identification of a single genomic region associated with seasonal river return timing in adult Scottish Atlantic salmon (*Salmo salar*), using a genome-wide association study. *Can J Fish Aquat Sci* 75:1427–1435. <https://doi.org/10.1139/cjfas-2017-0293>
- Caye K, Jumentier B, Lepeule J, François O (2019) LFMM 2: Fast and accurate inference of gene-environment associations in genome-wide studies. *Mol Biol Evol* 36:852–860. <https://doi.org/10.1093/molbev/msz008>
- Cayuela H, Rougemont Q, Laporte M, et al (2020) Shared ancestral polymorphisms and chromosomal rearrangements as potential drivers of local adaptation in a marine fish. *Mol Ecol* 29:2379–2398. <https://doi.org/10.1111/mec.15499>
- Chaput G (2012) Overview of the status of Atlantic salmon (*Salmo salar*) in the North Atlantic and trends in marine mortality. *ICES J Mar Sci* 69:1538–1548. <https://doi.org/10.1093/icesjms/fst048>
- Clark RD, Catalano KA, Fitz KS, et al (2023) The practice and promise of temporal genomics for measuring evolutionary responses to global change. *Mol Ecol Resour* 1–17. <https://doi.org/10.1111/1755-0998.13789>
- Consuegra S, De Leániz CG, Serdio A, Verspoor E (2005) Selective exploitation of early running fish may induce genetic and phenotypic changes in Atlantic salmon. *J Fish Biol* 67:129–145. <https://doi.org/10.1111/j.0022-1112.2005.00844.x>
- Cordoleani F, Sturrock A, Fitzgerald A, et al (2021) Threatened salmon rely on a rare life history strategy in a modified and warming landscape. Prepr available Res Sq 1–18
- Czorlich Y, Aykanat T, Erkinaro J, et al (2022) Rapid evolution in salmon life history induced by direct and indirect effects of fishing. *Science* (80-) 376:420–423. <https://doi.org/10.1126/science.abg5980>
- Czorlich Y, Aykanat T, Erkinaro J, et al (2018a) Rapid sex-specific evolution of age at maturity is shaped by genetic architecture in Atlantic salmon. *Nat Ecol Evol* 2:1800–1807. <https://doi.org/10.1038/s41559-018-0681-5>
- Czorlich Y, Aykanat T, Erkinaro J, et al (2018b) Rapid sex-specific evolution of age at maturity is shaped by genetic architecture in Atlantic salmon. *Nat Ecol Evol* 2:1800–1807. <https://doi.org/10.1038/s41559-018-0681-5>
- De-Kayne R, Selz OM, Marques DA, et al (2022) Genomic architecture of adaptive radiation and hybridization in Alpine whitefish. *Nat Commun* 13:1–13. <https://doi.org/10.1038/s41467-022-32181-8>
- de Villemereuil P, Gaggiotti OE (2015) A new FST-based method to uncover local adaptation using environmental variables. *Methods Ecol Evol* 6:1248–1258. <https://doi.org/10.1111/2041-210X.12418>
- Des Roches S, Post DM, Turley NE, et al (2018) The ecological importance of intraspecific variation. *Nat Ecol Evol* 2:57–64. <https://doi.org/10.1038/s41559-017-0402-5>

- Dionne M, Caron F, Dodson JJ, Bernatchez L (2009) Comparative survey of within-river genetic structure in Atlantic salmon; Relevance for management and conservation. *Conserv Genet* 10:869–879. <https://doi.org/10.1007/s10592-008-9647-5>
- Dionne M, Caron F, Dodson JJ, Bernatchez L (2008) Landscape genetics and hierarchical genetic structure in Atlantic salmon: The interaction of gene flow and local adaptation. *Mol Ecol* 17:2382–2396. <https://doi.org/10.1111/j.1365-294X.2008.03771.x>
- Elmer KR (2016) Genomic tools for new insights to variation, adaptation, and evolution in the salmonid fishes: a perspective for charr. *Hydrobiologia* 783:191–208. <https://doi.org/10.1007/s10750-015-2614-5>
- Erkinaro J, Czorlich Y, Orell P, et al (2019) Life history variation across four decades in a diverse population complex of atlantic salmon in a large subarctic river. *Can J Fish Aquat Sci* 76:42–55. <https://doi.org/10.1139/cjfas-2017-0343>
- Excoffier L, Hofer T, Foll M (2009) Detecting loci under selection in a hierarchically structured population. *Heredity (Edinb)* 103:285–298. <https://doi.org/10.1038/hdy.2009.74>
- Forester BR, Lasky JR, Wagner HH, Urban DL (2018) Comparing methods for detecting multilocus adaptation with multivariate genotype–environment associations. *Mol Ecol* 27:2215–2233. <https://doi.org/10.1111/mec.14584>
- Fraser DJ, Weir LK, Bernatchez L, et al (2011) Extent and scale of local adaptation in salmonid fishes: Review and meta-analysis. *Heredity (Edinb)* 106:404–420. <https://doi.org/10.1038/hdy.2010.167>
- Frankham R et al (2017) Genetic management of fragmented animal and plant populations. Oxford University Press, Oxford
- Fuentes-Pardo AP, Farrell ED, Pettersson ME, et al (2023) The genomic basis and environmental correlates of local adaptation in the Atlantic horse mackerel (*Trachurus trachurus*). *Evol Appl* 16:1201–1219. <https://doi.org/10.1111/eva.13559>
- Funk WC, McKay JK, Hohenlohe PA, Allendorf FW (2012) Harnessing genomics for delineating conservation units. *Trends Ecol Evol* 27:489–496. <https://doi.org/10.1016/j.tree.2012.05.012>
- Gabián M, Morán P, Saura M, Carvajal-Rodríguez A (2022) Detecting Local Adaptation between North and South European Atlantic Salmon Populations. *Biology (Basel)* 11:1–21. <https://doi.org/10.3390/biology11060933>
- Garcia De Leaniz C, Fleming IA, Einum S, et al (2007) A critical review of adaptive genetic variation in Atlantic salmon: Implications for conservation. *Biol Rev* 82:173–211. <https://doi.org/10.1111/j.1469-185X.2006.00004.x>
- Gautier M (2015) Genome-wide scan for adaptive divergence and association with population-specific covariates. *Genetics* 201:1555–1579. <https://doi.org/10.1534/genetics.115.181453>
- Gharrett AJ, Joyce J, Smoker WW (2013) Fine-scale temporal adaptation within a salmonid population: Mechanism and consequences. *Mol Ecol* 22:4457–4469. <https://doi.org/10.1111/mec.12400>
- Habel JC, Husemann M, Finger A, et al (2014) The relevance of time series in molecular ecology and conservation biology. *Biol Rev* 89:484–492. <https://doi.org/10.1111/brv.12068>
- Hahn MW (2019) Molecular population genetics. Oxford University Press, Oxford.
- Han F, Jamsandekar M, Pettersson ME, et al (2020) Ecological adaptation in atlantic herring is associated with large shifts in allele frequencies at hundreds of LOCI. *Elife* 9:1–20. <https://doi.org/10.7554/ELIFE.61076>
- Handford P, Bell G, Reimchen T (1977) A Gillnet Fishery Considered as an Experiment in Artificial Selection. *J Fish Board Canada* 34:954–961

- Harvey AC, Tang Y, Wennevik V, et al (2017) Timing is everything: Fishing-season placement may represent the most important angling-induced evolutionary pressure on Atlantic salmon populations. *Ecol Evol* 7:7490–7502. <https://doi.org/10.1002/ece3.3304>
- Hecht BC, Matala AP, Hess JE, Narum SR (2015) Environmental adaptation in Chinook salmon (*Oncorhynchus tshawytscha*) throughout their North American range. *Mol Ecol* 24:5573–5595. <https://doi.org/10.1111/mec.13409>
- Heino J, Culp JM, Erkinaro J, et al (2020) Abruptly and irreversibly changing Arctic freshwaters urgently require standardized monitoring. *J Appl Ecol* 57:1192–1198. <https://doi.org/10.1111/1365-2664.13645>
- Heino M, Díaz Pauli B, Dieckmann U (2015) Fisheries-Induced Evolution. *Annu Rev Ecol Evol Syst* 46:461–480. <https://doi.org/10.1146/annurev-ecolsys-112414-054339>
- Heino MT, Nyman T, Palo JU, et al (2023) Museum specimens of a landlocked pinniped reveal recent loss of genetic diversity and unexpected population connections. *Ecol Evol* 13:1–16. <https://doi.org/10.1002/ece3.9720>
- 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. *Balt. Sea Environ. Proc. No. 126A*.
- HELCOM Red List Fish and Lamprey Species Expert Group 2013. <https://helcom.fi/wp-content/uploads/2019/08/HELCOM-Red-List-Salmo-salar.pdf> Retrieved on 10 September 2023.
- Hess JE, Zendt JS, Matala AR, Narum SR (2016) Genetic basis of adult migration timing in anadromous steelhead discovered through multivariate association testing. *Proc R Soc B Biol Sci* 283:. <https://doi.org/10.1098/rspb.2015.3064>
- Hilborn R, Quinn TP, Schindler DE, Rogers DE (2003) Biocomplexity and fisheries sustainability. *Proc Natl Acad Sci U S A* 100:6564–6568. <https://doi.org/10.1073/pnas.1037274100>
- Hoban S, Bruford M, D’Urban Jackson J, et al (2020) Genetic diversity targets and indicators in the CBD post-2020 Global Biodiversity Framework must be improved. *Biol Conserv* 248:108654. <https://doi.org/10.1016/j.biocon.2020.108654>
- Hoban S, Campbell CD, da Silva JM, et al (2021) Genetic diversity is considered important but interpreted narrowly in country reports to the Convention on Biological Diversity: Current actions and indicators are insufficient. *Biol Conserv* 261:. <https://doi.org/10.1016/j.biocon.2021.109233>
- Hoban S, Kelley JL, Lotterhos KE, et al (2016) Finding the genomic basis of local adaptation: Pitfalls, practical solutions, and future directions. *Am Nat* 188:379–397. <https://doi.org/10.1086/688018>
- Hoelzel AR, Bruford MW, Fleischer RC (2019) Conservation of adaptive potential and functional diversity. *Conserv Genet* 20:1–5. <https://doi.org/10.1007/s10592-019-01151-x>
- Hohenlohe PA, Funk WC, Rajora OP (2021) Population genomics for wildlife conservation and management. *Mol Ecol* 30:62–82. <https://doi.org/10.1111/mec.15720>
- Hoikkala A, Poikela N (2022) Adaptation and ecological speciation in seasonally varying environments at high latitudes: *Drosophila virilis* group. *Fly (Austin)* 16:85–104. <https://doi.org/10.1080/19336934.2021.2016327>
- Hughes AR, Inouye BD, Johnson MTJ, et al (2008) Ecological consequences of genetic diversity. *Ecol Lett* 11:609–623. <https://doi.org/10.1111/j.1461-0248.2008.01179.x>
- Hutchings JA, Kuparinen A (2020) Implications of fisheries-induced evolution for population recovery: Refocusing the science and refining its communication. *Fish Fish* 21:453–464. <https://doi.org/10.1111/faf.12424>

- ICES (2023) Baltic Salmon and Trout Assessment Working Group (WGBAST). ICES Sci Reports 5:465 pp.
- ICES (2020) EU request on evaluation of a draft multiannual plan for the Baltic salmon stock and the fisheries exploiting the stock. Rep ICES Advis Comm ICES Advic:
- Ikonen E (2006) The role of the feeding migration and diet of Atlantic salmon (*Salmo salar* L.) in yolk-sack-fry mortality (M74) in the Baltic Sea. PhD thesis, University of Helsinki, Finland.
- IPBES (2019): Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. S. Díaz *et al.* (eds.). IPBES secretariat, Bonn, Germany. 56 pages.
- Jacobson P, Gårdmark A, Huss M (2020) Population and size-specific distribution of Atlantic salmon *Salmo salar* in the Baltic Sea over five decades. *J Fish Biol* 96:408–417. <https://doi.org/10.1111/jfb.14213>
- Jansson H (1993) Allozyme evidence for local populations of Atlantic salmon (*Salmo salar* L.) in the Kalix River, northern Sweden. *ICES* 1–15
- Jarkko R, Juslén A, Kekkonen M, Aspi J (2019) Opas geneettiseen monimuotoisuuteen - Esimerkkejä Suomen luonnosta. Luonnontieteellinen keskusmuseo, Helsingin yliopisto & Oulun yliopisto. <http://hdl.handle.net/10138/301770>
- Jenkins DG, Carey M, Czerniewska J, et al (2010) A meta-analysis of isolation by distance: Relic or reference standard for landscape genetics? *Ecography (Cop)* 33:315–320. <https://doi.org/10.1111/j.1600-0587.2010.06285.x>
- Jensen AJ, Hagen IJ, Czorlich Y, et al (2022a) Large-effect loci mediate rapid adaptation of salmon body size after river regulation. *Proc Natl Acad Sci U S A* 119:1–8. <https://doi.org/10.1073/pnas.2207634119>
- Jensen EL, Díez-del-Molino D, Gilbert MTP, et al (2022b) Ancient and historical DNA in conservation policy. *Trends Ecol Evol* xx:1–10. <https://doi.org/10.1016/j.tree.2021.12.010>
- Johnston SE, Gratten J, Berenos C, et al (2013) Life history trade-offs at a single locus maintain sexually selected genetic variation. *Nature* 502:93–95. <https://doi.org/10.1038/nature12489>
- Jokikokko E, Kallio-Nyberg I, Jutila E (2004) The timing, sex and age composition of the wild and reared Atlantic salmon ascending the Simojoki River, northern Finland. *J Appl Ichthyol* 20:37–42. <https://doi.org/10.1111/j.1439-0426.2004.00491.x>
- Jonsson B, Jonsson N (2009) A review of the likely effects of climate change on anadromous Atlantic salmon *Salmo salar* and brown trout *Salmo trutta*, with particular reference to water temperature and flow. *J Fish Biol* 75:2381–2447. <https://doi.org/10.1111/j.1095-8649.2009.02380.x>
- Kalananthan T, Folkedal O, Gomes AS, et al (2023) Impact of long-term fasting on the stomach-hypothalamus appetite regulating genes in Atlantic salmon postsmolts. *Aquaculture* 563:1–10. <https://doi.org/10.1016/j.aquaculture.2022.738917>
- Kalananthan T, Lai F, Gomes AS, et al (2020) The Melanocortin System in Atlantic Salmon (*Salmo salar* L.) and Its Role in Appetite Control. *Front Neuroanat* 14:1–15. <https://doi.org/10.3389/fnana.2020.00048>
- Kardos M, Shafer ABA (2018) The Peril of Gene-Targeted Conservation. *Trends Ecol Evol* 33:827–839. <https://doi.org/10.1016/j.tree.2018.08.011>
- Karlsson L, Karlström Ö (1994) The Baltic salmon (*Salmo salar* L.): its history, present situation and future. *Dana* 10:61–85

- Kess T, Lehnert SJ, Bentzen P, et al (2022) Parallel genomic basis of age at maturity across spatial scales in Atlantic Salmon. *bioRxiv* 1–38
- Kokko J (1864) Lohen h t huuto asukkaille Tornion joen rannoilla. Retrieved from <https://www.suomenkalakirjasto.fi/wp-content/uploads/2023/09/Hatahuuto-asukkaille-Tornion-joen-rannoilla.pdf>
- Koljonen M-L (2006) Annual changes in the proportions of wild and hatchery Atlantic salmon (*Salmo salar*) caught in the Baltic Sea. *ICES J Mar Sci* 63:1274–1285. <https://doi.org/10.1016/j.icesjms.2006.04.010>
- Koljonen ML, McKinnell S (1996) Assessing seasonal changes in stock composition of Atlantic salmon catches in the Baltic Sea with genetic stock identification. *J Fish Biol* 49:998–1018. <https://doi.org/10.1006/jfbi.1996.0228>
- Konijnendijk N, Shikano T, Daneels D, et al (2015) Signatures of selection in the three-spined stickleback along a small-scale brackish water - freshwater transition zone. *Ecol Evol* 5:4174–4186. <https://doi.org/10.1002/ece3.1671>
- Kovach RP, Ellison SC, Pyare S, Tallmon DA (2015) Temporal patterns in adult salmon migration timing across southeast Alaska. *Glob Chang Biol* 21:1821–1833. <https://doi.org/10.1111/gcb.12829>
- Kovach RP, Gharrett AJ, Tallmon DA (2012) Genetic change for earlier migration timing in a pink salmon population. *Proc R Soc B Biol Sci* 279:3870–3878. <https://doi.org/10.1098/rspb.2012.1158>
- Kuparinen A, Hutchings JA (2017) Genetic architecture of age at maturity can generate divergent and disruptive harvest-induced evolution. *Philos Trans R Soc B Biol Sci* 372:. <https://doi.org/10.1098/rstb.2016.0035>
- Laikre L (2010) Genetic diversity is overlooked in international conservation policy implementation. *Conserv Genet* 11:349–354. <https://doi.org/10.1007/s10592-009-0037-4>
- Lank D, Smith C, Hanotte O, et al (1995) Genetic polymorphisms and alternative mating behaviour in lekking ruff. *378:223–224*
- Lank DB, Farrell LL, Burke T, et al (2013) A dominant allele controls development into female mimic male and diminutive female ruffs. *Biol Lett* 9:15–18. <https://doi.org/10.1098/rsbl.2013.0653>
- Layton KKS, Snelgrove PVR, Dempson JB, et al (2021) Genomic evidence of past and future climate-linked loss in a migratory Arctic fish. *Nat Clim Chang* 11:158–165. <https://doi.org/10.1038/s41558-020-00959-7>
- Le Moan A, Bekkevold D, Hemmer-Hansen J (2021) Evolution at two time frames: ancient structural variants involved in post-glacial divergence of the European plaice (*Pleuronectes platessa*). *Heredity* (Edinb) 126:668–683. <https://doi.org/10.1038/s41437-020-00389-3>
- Leigh DM, Hendry AP, V zquez-Dom nguez E, Friesen VL (2019) Estimated six per cent loss of genetic variation in wild populations since the industrial revolution. *Evol Appl* 12:1505–1512. <https://doi.org/10.1111/eva.12810>
- Mamoozadeh NR, Whiteley AR, Letcher BH, et al (2023) A new genomic resource to enable standardized surveys of SNPs across the native range of brook trout (*Salvelinus fontinalis*). *Mol Ecol Resour* 1–20. <https://doi.org/10.1111/1755-0998.13853>
- Meirmans PG (2012) The trouble with isolation by distance. *Mol Ecol* 21:2839–2846. <https://doi.org/10.1111/j.1365-294X.2012.05578.x>
- Mimura M, Yahara T, Faith DP, et al (2017) Understanding and monitoring the consequences of human impacts on intraspecific variation. *Evol Appl* 10:121–139.

<https://doi.org/10.1111/eva.12436>

- Mobley KB, Aykanat T, Czorlich Y, et al (2021) Maturation in Atlantic salmon (*Salmo salar*, Salmonidae): a synthesis of ecological, genetic, and molecular processes
- Mondol S, Bruford MW, Ramakrishnan U (2013) Demographic loss , genetic structure and the conservation implications for Indian tigers Receive free email alerts when new articles cite this article - sign up in the box at the t
- Moore JS, Bourret V, Dionne M, et al (2014) Conservation genomics of anadromous Atlantic salmon across its North American range: Outlier loci identify the same patterns of population structure as neutral loci. *Mol Ecol* 23:5680–5697. <https://doi.org/10.1111/mec.12972>
- Myrvold KM, Mawle GW, Aas Ø (2019) The social, economic and cultural values of wild Atlantic salmon. A review of the literature for the period 2009-2019 and an assessment of changes in values. *NINA Rep* 1668
- Nakahama N (2021) Museum specimens: An overlooked and valuable material for conservation genetics. *Ecol Res* 36:13–23. <https://doi.org/10.1111/1440-1703.12181>
- Nielsen EE, Hansen MM (2008) Waking the dead: The value of population genetic analyses of historical samples. *Fish Fish* 9:450–461. <https://doi.org/10.1111/j.1467-2979.2008.00304.x>
- Niemelä E, Orell P, Erkinaro J, et al (2006) Previously spawned Atlantic salmon ascend a large subarctic river earlier than their maiden counterparts. *J Fish Biol* 69:1151–1163. <https://doi.org/10.1111/j.1095-8649.2006.01190.x>
- Norland S, Eilertsen M, Rønnestad I, et al (2023) Mapping key neuropeptides involved in the melanocortin system in Atlantic salmon (*Salmo salar*) brain. *J Comp Neurol* 531:89–115. <https://doi.org/10.1002/cne.25415>
- Oksanen, J., Simpson, G. L., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Solymos, P., Stevens, M. H. H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., ... Weedon, J. (2022). *vegan: Community Ecology Package*. <https://cran.r-project.org/web/packages/vegan/index.html>
- Oomen RA, Kuparinen A, Hutchings JA (2020) Consequences of Single-Locus and Tightly Linked Genomic Architectures for Evolutionary Responses to Environmental Change. *J Hered* 319–332. <https://doi.org/10.1093/jhered/esaa020>
- Östergren J, Palm S, Gilbey J, et al (2021) A century of genetic homogenization in Baltic salmon – evidence from archival DNA. *Proceedings of the Royal Society B: Biological Sciences*, 288, 20203147. <https://doi.org/10.1098/rspb.2020.3147>
- Palm S, Romakkaniemi A, Dannewitz J, et al (2023) Torneälvens bestånd av lax, havsöring, vandringsik och harr – gemensamt svensk-finskt biologiskt underlag för bedömning av lämpliga fiskeregler under 2023. 1:1–52
- Palmé A, Wenneström L, Guban P, et al (2012) Compromising Baltic L salmon genetic diversity - conservation genetic risks associated with compensatory releases of salmon in the Baltic Sea. *Havs- och vattenmyndighetens Rapp* 18:
- Pavlidis P, Jensen JD, Stephan W, Stamatakis A (2012) A critical assessment of storytelling: Gene ontology categories and the importance of validating genomic scans. *Mol Biol Evol* 29:3237–3248. <https://doi.org/10.1093/molbev/mss136>
- Paz-Vinas I, Loot G, Stevens VM, Blanchet S (2015) Evolutionary processes driving spatial patterns of intraspecific genetic diversity in river ecosystems. *Mol Ecol* 24:4586–4604. <https://doi.org/10.1111/mec.13345>

- Pearse DE, Barson NJ, Nome T, et al (2019) Sex-dependent dominance maintains migration supergene in rainbow trout. *Nat Ecol Evol* 3:1731–1742. <https://doi.org/10.1038/s41559-019-1044-6>
- Pinsky ML, Maria A, Helmersen C, et al (2021) Genomic stability through time despite decades of exploitation in cod on both sides of the Atlantic. 1–6. <https://doi.org/10.1073/pnas.2025453118>
- Pinsky ML, Palumbi SR (2014) Meta-analysis reveals lower genetic diversity in overfished populations. *Mol Ecol* 23:29–39. <https://doi.org/10.1111/mec.12509>
- Pohja-Mykrä M, Matilainen A, Kujala S, et al (2018) Erätalouteen liittyvän yritystoiminnan nykytila ja kehittämisellätykset
- Pokki H, Artell J, Mikkola J, et al (2018) Valuing recreational salmon fishing at a remote site in Finland: A travel cost analysis. *Fish Res* 208:145–156. <https://doi.org/10.1016/j.fishres.2018.07.013>
- Primmer CR (2011) Genetics of local adaptation in salmonid fishes. *Heredity (Edinb)* 106:401–403. <https://doi.org/10.1038/hdy.2010.158>
- Primmer CR, Veselov AJ, Zubchenko A, et al (2006) Isolation by distance within a river system: Genetic population structuring of Atlantic salmon, *Salmo salar*, in tributaries of the Varzuga River in northwest Russia. *Mol Ecol* 15:653–666. <https://doi.org/10.1111/j.1365-294X.2005.02844.x>
- Prince DJ, O'Rourke SM, Thompson TQ, et al (2017) The evolutionary basis of premature migration in Pacific salmon highlights the utility of genomics for informing conservation. *Sci Adv* 3:. <https://doi.org/10.1126/sciadv.1603198>
- Pritchard VL, Mäkinen H, Vähä J-P, et al (2018) Genomic signatures of fine-scale local selection in Atlantic salmon suggest involvement of sexual maturation, energy homeostasis and immune defence-related genes. *Mol Ecol*. <https://doi.org/10.1111/mec.14705>
- Privé F, Luu K, Vilhjálmsson BJ, et al (2020) Performing Highly Efficient Genome Scans for Local Adaptation with R Package pcadapt Version 4. *Mol Biol Evol* 37:2153–2154. <https://doi.org/10.1093/molbev/msaa053>
- Prowse TD, Wrona FJ, Reist JD, et al (2006) Climate change effects on hydroecology of arctic freshwater ecosystems. *Ambio* 35:347–358. [https://doi.org/10.1579/0044-7447\(2006\)35\[347:CCEOHO\]2.0.CO;2](https://doi.org/10.1579/0044-7447(2006)35[347:CCEOHO]2.0.CO;2)
- Quinn TP (1993) A review of homing and straying of wild and hatchery-produced salmon. *Fish Res* 18:29–44. [https://doi.org/10.1016/0165-7836\(93\)90038-9](https://doi.org/10.1016/0165-7836(93)90038-9)
- Quinn TP, McGinnity P, Cross TF (2006) Long-term declines in body size and shifts in run timing of Atlantic salmon in Ireland. *J Fish Biol* 1713–1730. <https://doi.org/10.1111/j.1095-8649.2006.01017.x>
- Quinn TP, McGinnity P, Reed TE (2016) The paradox of “premature migration” by adult anadromous salmonid fishes: Patterns and hypotheses. *Can J Fish Aquat Sci* 73:1015–1030. <https://doi.org/10.1139/cjfas-2015-0345>
- Quintela M, Kvamme C, Bekkevold D, et al (2020) Genetic analysis redraws the management boundaries for the European sprat. *Evol Appl* 13:1906–1922. <https://doi.org/10.1111/eva.12942>
- Raeymaekers JAM, Maes GE, Geldof S, et al (2008) Modeling genetic connectivity in sticklebacks as a guideline for river restoration. *Evol Appl* 1:475–488. <https://doi.org/10.1111/j.1752-4571.2008.00019.x>
- Rellstab C, Gugerli F, Eckert AJ, et al (2015) A practical guide to environmental association analysis in landscape genomics. *Mol Ecol* 24:4348–4370.

<https://doi.org/10.1111/mec.13322>

- Romakkaniemi A, Perä I, Karlsson L, et al (2003) Development of wild Atlantic salmon stocks in the rivers of the northern Baltic Sea in response to management measures. *ICES J Mar Sci* 60:329–342. [https://doi.org/10.1016/S1054-3139\(03\)00020-1](https://doi.org/10.1016/S1054-3139(03)00020-1)
- Rutter C (1902) Natural history of the Quinnat Salmon. A Report of Investigations in the Sacramento River, 1896-1901. Retrieved from <https://spo.nmfs.noaa.gov/content/natural-history-quinnat-salmon>
- Säisä M, Koljonen ML, Tähtinen J (2003) Genetic changes in Atlantic salmon stocks since historical times and the effective population size of a long-term captive breeding programme. *Conserv Genet* 4:613–627. <https://doi.org/10.1023/A:1025680002296>
- Saura M, Morán P, Brotherstone S, et al (2010) Predictions of response to selection caused by angling in a wild population of Atlantic salmon (*Salmo salar*). *Freshw Biol* 55:923–930. <https://doi.org/10.1111/j.1365-2427.2009.02346.x>
- Schindler DE, Hilborn R, Chasco B, et al (2010) Population diversity and the portfolio effect in an exploited species. *Nature* 465:609–612. <https://doi.org/10.1038/nature09060>
- Schmidt C, Hoban S, Jetz W (2023) Conservation macrogenetics: harnessing genetic data to meet conservation commitments. *Trends Genet* 1–14. <https://doi.org/10.1016/j.tig.2023.08.002>
- Shafer ABA, Wolf JBW, Alves PC, et al (2015) Genomics and the challenging translation into conservation practice. *Trends Ecol Evol* 30:78–87. <https://doi.org/10.1016/j.tree.2014.11.009>
- Shearer WM (1990) The Atlantic salmon (*Salmo salar* L.) of the North Esk with particular reference to the relationship between both river and sea age and time of return to home waters. *Fish Res* 10:93–123. [https://doi.org/10.1016/0165-7836\(90\)90017-P](https://doi.org/10.1016/0165-7836(90)90017-P)
- Sinclair-Waters M, Nome T, Wang J, et al (2022) Dissecting the loci underlying maturation timing in Atlantic salmon using haplotype and multi-SNP based association methods. *Heredity (Edinb)* 129:356–365. <https://doi.org/10.1038/s41437-022-00570-w>
- Sinclair-Waters M, Ødegård J, Korsvoll SA, et al (2020) Beyond large - effect loci : large - scale GWAS reveals a mixed large - effect and polygenic architecture for age at maturity of Atlantic salmon. *Genet Sel Evol* 1–11. <https://doi.org/10.1186/s12711-020-0529-8>
- Slatkin M (1993) Isolation By Distance In Equilibrium and Non-Equilibrium Populations. *Evolution (N Y)* 47:264–279
- Ståhl G (1981) Genetic differentiation among natural populations of Atlantic salmon (*Salmo salar*) in northern Sweden. *Ecol Bull* 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. [https://doi.org/10.1016/0044-8486\(83\)90383-6](https://doi.org/10.1016/0044-8486(83)90383-6)
- Szpiech ZA (2022) Selscan 2.0: Scanning for Sweeps in Unphased Data. *bioRxiv* 2021.10.22.465497
- Szpiech ZA, Hernandez RD (2014) Selscan: An efficient multithreaded program to perform EHH-based scans for positive selection. *Mol Biol Evol* 31:2824–2827. <https://doi.org/10.1093/molbev/msu211>
- Tamario C, Sunde J, Petersson E, et al (2019) Ecological and Evolutionary Consequences of Environmental Change and Management Actions for Migrating Fish. *Front Ecol Evol* 7:1–24. <https://doi.org/10.3389/fevo.2019.00271>
- Thompson TQ, Renee Bellinger M, O'Rourke SM, et al (2019) Anthropogenic habitat alteration leads to rapid loss of adaptive variation and restoration potential in wild salmon

- populations. *Proc Natl Acad Sci U S A* 116:177–186. <https://doi.org/10.1073/pnas.1811559115>
- Thorstad EB, Bliss D, Breau C, et al (2021) Atlantic salmon in a rapidly changing environment—Facing the challenges of reduced marine survival and climate change. *Aquat Conserv Mar Freshw Ecosyst* 31:2654–2665. <https://doi.org/10.1002/aqc.3624>
- Thorstad EB, Whoriskey F, Rikardsen AH, Aarestrup K (2011) Aquatic Nomads: The Life and Migrations of the Atlantic Salmon. In: Aas Ø, Einum S, Klemetsen A, Skurdal J (eds) *Atlantic Salmon Ecology*, First edit. Blackwell Publishing Ltd., pp 31–62
- Tigano A, Russello MA (2022) The genomic basis of reproductive and migratory behaviour in a polymorphic salmonid. *Mol Ecol* 31:6588–6604. <https://doi.org/10.1111/mec.16724>
- Uusi-Heikkilä S, Whiteley AR, Kuparinen A, et al (2015) The evolutionary legacy of size-selective harvesting extends from genes to populations. *Evol Appl* 8:597–620. <https://doi.org/10.1111/eva.12268>
- Vähä J-P, Erkinaro J, Falkegård M, et al (2017) Genetic stock identification of Atlantic salmon and its evaluation in a large population complex. *Can J Fish Aquat Sci*. <https://doi.org/10.1139/cjfas-2015-0606>
- Vähä J-P, Erkinaro J, Niemelä E, Primmer CR (2007) Life-history and habitat features influence the within-river genetic structure of Atlantic salmon. *Mol Ecol*. <https://doi.org/10.1111/j.1365-294X.2007.03329.x>
- van Wijk SJ, Taylor MI, Creer S, et al (2013) Experimental harvesting of fish populations drives genetically based shifts in body size and maturation. *Front Ecol Environ* 11:181–187. <https://doi.org/10.1890/120229>
- Vasemägi A, Gross R, Paaver T, et al (2005) Extensive immigration from compensatory hatchery releases into wild Atlantic salmon population in the Baltic sea: Spatio-temporal analysis over 18 years. *Heredity (Edinb)* 95:76–83. <https://doi.org/10.1038/sj.hdy.6800693>
- Wang IJ, Bradburd GS (2014) Isolation by environment. *Mol Ecol* 23:5649–5662. <https://doi.org/10.1111/mec.12938>
- Waples RS, Ford MJ, Nichols K, et al (2022) Implications of Large-Effect Loci for Conservation: A Review and Case Study with Pacific Salmon. *J Hered* 113:121–144. <https://doi.org/10.1093/jhered/esab069>
- Waters CD, Clemento A, Aykanat T, et al (2021) Heterogeneous genetic basis of age at maturity in salmonid fishes. *Mol Ecol* 1435–1456. <https://doi.org/10.1111/mec.15822>
- Watson KB, Lehnert SJ, Bentzen P, et al (2022) Environmentally associated chromosomal structural variation influences fine-scale population structure of Atlantic Salmon (*Salmo salar*). *Mol Ecol* 31:1057–1075. <https://doi.org/10.1111/mec.16307>
- Wellband K, Mérot C, Linnansaari T, et al (2018) Chromosomal fusion and life history-associated genomic variation contribute to within-river local adaptation of Atlantic salmon. *Mol Ecol* 1439–1459. <https://doi.org/10.1111/mec.14965>
- Whitlock MC, Lotterhos KE (2015) Reliable detection of loci responsible for local adaptation: Inference of a null model through trimming the distribution of FST. *Am Nat* 186:S24–S36. <https://doi.org/10.1086/682949>
- Whitlock R, Mäntyniemi S, Palm S, et al (2018) Integrating genetic analysis of mixed populations with a spatially explicit population dynamics model. *Methods Ecol Evol* 2018:1017–1035. <https://doi.org/10.1111/2041-210X.12946>
- Whitlock RE, Pakarinen T, Palm S, et al (2021) Trade-offs among spatio-temporal management actions for a mixed-stock fishery revealed by Bayesian decision analysis. *ICES J Mar Sci* 78:3625–3638. <https://doi.org/10.1093/icesjms/fsab203>

- Willis SC, Hess JE, Fryer JK, et al (2020) Steelhead (*Oncorhynchus mykiss*) lineages and sexes show variable patterns of association of adult migration timing and age-at-maturity traits with two genomic regions. *Evol Appl* 1–21. <https://doi.org/10.1111/eva.13088>
- Xuereb A, Rougemont Q, Dallaire X, et al (2022) Re-evaluating Coho salmon (*Oncorhynchus kisutch*) conservation units in Canada using genomic data. *Evol Appl* 15:1925–1944. <https://doi.org/10.1111/eva.13489>
- Zueva KJ, Lumme J, Veselov AE, et al (2021) Population genomics reveals repeated signals of adaptive divergence in the Atlantic salmon of north-eastern Europe. *J Evol Biol* 34:866–878. <https://doi.org/10.1111/jeb.13732>