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A large, stylized graphic of a salmon tail, rendered in a light teal color, occupies the left and center portions of the cover. The tail is shown from a dorsal view, with the central lobe and the radiating rays of the tail fin clearly defined.

POPULATION DYNAMICS
AND EVOLUTIONARY
GENETICS OF LIFE
HISTORY VARIATION IN
ATLANTIC SALMON

Yann Czorlich



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POPULATION DYNAMICS AND EVOLUTIONARY GENETICS OF LIFE HISTORY VARIATION IN ATLANTIC SALMON

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Tiivistelmä

Kalastuksen kohteena olevien kalakantojen hoidossa tarvitaan tietoja kannan runsauden ja elinkierto- ja vaihtelun vaihtelusta. Atlantin lohella (*Salmo salar*) on suuri kulttuurinen, ekologinen ja taloudellinen merkitys, ja se ylläpitää merkittävää vapaa-ajan-, kotitarve- ja ammattikalastusta. Monet uhkatekijät (esim. kasvatettujen lohien vaikutukset luonnonlohen perimään, ilmastonmuutos, ylikalastus) ovat johtaneet lohikantojen tilan heikkenemiseen ja muutoksiin niiden elinkierto- ja vaihtelussa. Pitkän aikavälin seuranta-aineistot yhdistettynä mallintamiseen ja nykyaikaisiin geneettisiin menetelmiin mahdollistavat tällaisten muutosten kuvaamisen ja auttavat niihin johtaneiden syiden löytämisessä. Tässä väitöskirjassa käytettiin Tenojolta vuosina 1975–2014 kerättyjä seuranta-aineistoja. Tenojoen lohi koostuu useista geneettisesti erilaistuneista osapopulaatioista ja Tenojoki tuottaa vuosittain Euroopan suurimpia lohien jokisaaliita. Tenon lohelta tavattiin 120 erilaista elinkierto- ja vaihtelun yhdistelmää, jotka koostuvat vaihteluista jokivaiheen kestossa (2–8 vuotta), merivuosisa (1–5 vuotta) ja aiempien kutukertojen yhdistelmissä (37 peräkkäisinä vuosina, 54 vuorovuosisin kutevien lohien elinkierto- ja vaihtelun yhdistelmää). Elinkierto- ja vaihtelun yhdistelmät vaihtelivat sekä alueellisesti Tenon eri osien välillä että ajallisesti; erityisesti suurten, kolme vuotta tai pidempään meressä viettäneiden lohien määrä on pienentynyt pitkällä aikavälillä. Tenon lohella havaittiin sopeutuvaa evoluutiota sukukypsyys- ja suhteen: *vgll3* -geenin myöhäisen sukukypsyuden alleelin frekvenssi pieneni 40 vuoden aikajänteellä 18%. Alleelifrekvenssin muutokset johtuivat todennäköisesti kalastuksen suorista ja epäsuorista vaikutuksista: sekä kokovalikoivien pyydysten käytöstä jokikalastuksessa, että lohien merkittävän mereisen ravintokohteen, villakuoreen, voimakkaasta kalastuksesta. Geneettisestä muutoksesta johtuva merkittävä fenotyypin muutos osoitettiin nimenomaan koiraslohisissa. Fenotyypin vaste geneettisen muutokseen vaihtelee sukupuolten välillä koska *vgll3* -geenin alleelien dominanssi- ja yhdysvaikutukset ovat sukupuoliriippuvaisia. Ikärakenteeltaan erilaisen Inarijoen lohipopulaation geneettinen muutos ei ollut yhtä suuri kuin Tenon pääuomassa, mikä luultavasti johtui ikärakenteeseen liittyvistä erilaisista valintapaineista. Utsjoen lohikannalle kehitettiin bayesilainen elinkierto- ja vaihtelun malli, jonka hierarkisen rakenteen ansioista sitä voidaan soveltaa myös populaatioihin, joista on käytettävissä Utsjokea vähemmän seuranta- ja tutkimustietoa. Monipuolista tietoa (esim. lohien videolaskennan tuloksia, asiantuntija-arvioita ja kirjallisuustietoja) käyttävää mallia, joka ottaa huomioon erilaiset epävarmuuden lähteet (esim. havaintojen ja prosessien virheet), voidaan hyödyntää määriteltäessä kannan tilan tavoitetasoja lohikantojen hoitoa varten ja arvioitaessa kannan tilaa suhteessa tavoitteisiin. Tässä väitöskirjassa yhdistetty ekologinen ja geneettinen tieto auttaa ymmärtämään Tenon lohikantojen monimuotoisuuden ja elinkierto- ja vaihtelun vaihtelua sekä niihin mahdollisesti vaikuttavia tekijöitä. Monipuolisten aineistojen yhdistämistä ekologis-evoluutiiviseen mallinnukseen voidaan kehittää edelleen jotta ekologis-evoluutiivisia yhteisvaikutuksia sekä niiden yhteyttä lohikantojen tilaan ja elinkykyyn ymmärrettäisiin entistä paremmin.

Abstract:

Knowledge about variation in abundance and life-history traits is necessary to manage exploited populations. Atlantic salmon, *Salmo salar*, has high cultural, ecological and economic importance, supporting subsistence, leisure and commercial fishing. This species has been exposed to numerous threats (e.g. introgression, climate change, overexploitation) leading to a global decrease in Atlantic salmon production and changes in life history traits. Historical collection of data and biological material coupled with modelling and recent advances in genetics may help in describing those changes and identifying potential causes. In this thesis, we used data and biological material collected from 1975 to 2014 in the northern European Teno river, which hosts a highly structured salmon population and yields one of the largest riverine salmon catches in Europe. We quantified a total of 120 different life history combinations in the Teno river, including variation in smolt age (2-8 years), age at maturity (1-5 years) and several forms of repeat (37) and alternate spawners (54). Life history traits varied both spatially and temporally, particularly the age at maturity with an important decline in the proportion of large salmon, maturing after three years at sea. We demonstrated adaptive evolution of age at maturity over 40 years in the main population of the Teno river by observing an 18% decrease in *vgll3* late maturation allele frequency, a genetic marker strongly associated with this trait. Changes in *vgll3* allele and genotype frequencies were likely to have been driven by direct and indirect effects of fishing, by intensively exploiting a salmon prey (capelin) and using selective fishing gears in the river. Only males clearly responded to genetic changes at the phenotypic level, with a strong decline in age at maturity. The consequences of changes in genotype frequencies on mean age at maturity may differ between sexes because of sex-dependent variation in *vgll3* additive and dominance effects. Furthermore, this sex-specific genetic architecture differed in a second population with contrasting age structure, likely affecting selection patterns. We finally developed a Bayesian life cycle model for salmon in Utsjoki, the largest tributary of the Teno river, which could later be extended to data-poor stocks using hierarchical structures. Such a model, including various sources of information (e.g. video counting, expert knowledge and literature) and accounting for different kind of uncertainty (e.g. observation and process errors), may be useful to provide reference points for management and evaluate attainment of objectives. The combined use of ecological and genetic data in this thesis improved our knowledge about the diversity and variation of life history traits in Teno river Atlantic salmon, along with potential factors affecting them. A further development would be to integrate both types of data in eco-evolutionary models to improve our understanding of the interaction between ecology and evolution and its consequences for population viability.

List of original publications:

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

- I Erkinaro*, J., Czorlich*, Y., Orell, P., Kuusela, J., Falkegård, M., Länsman, M., Pulkkinen, H., Primmer, C. R., & Niemelä, E. (2019). Life history variation across four decades in a diverse population complex of Atlantic salmon in a large subarctic river. *Canadian Journal of Fisheries and Aquatic Sciences*, 76, 42–55.
- II Czorlich, Y., Aykanat, T., Erkinaro, J., Orell, P., & Primmer, C. R. (2018). Rapid sex-specific evolution of age at maturity is shaped by genetic architecture in Atlantic salmon. *Nature Ecology & Evolution*, 2, 1800–1807.
- III Czorlich, Y., Aykanat, T., Erkinaro, J., Orell, P., & Primmer, C. R. (2019). Evolution in salmon life-history induced by direct and indirect effects of fishing. *Manuscript*.
- IV Czorlich, Y., Pulkkinen, H., Länsman, M., Falkegård, M., & Erkinaro, J. (2019). Integrated Bayesian life cycle model applied to Atlantic salmon from the Utsjoki river. *Manuscript*.

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Introduction:

Knowledge about factors influencing populations' abundance and life history traits is essential for the conservation of threatened and/or exploited species. By incorporating various sources of available data, population dynamics models constitute useful tools to improve our understanding of phenomena and obtain predictions under different scenarios (Parent & Rivot, 2012). Evaluating and conserving the adaptive potential of populations (i.e. ability to respond to selection) is also considered decisive in population management and conservation (Eizaguirre & Baltazar-soares, 2014). Integrating knowledge about ecological and evolutionary mechanisms would improve the evaluation of persistence probability in populations facing rapidly changing environments (Reed et al., 2011).

The increasing rate of climate change and other growing anthropogenic pressures may require populations to move, acclimate or adapt in order to persist. Low dispersal capacity, fragmented habitats or the absence of suitable environments nearby may limit the ability of individuals to migrate to optimal environmental conditions (Mantyka-Pringle et al., 2012; Schloss et al., 2012). Phenotypic plasticity, i.e. the ability to express a different phenotype from the same genotype, may engender quick intra-generation responses potentially reducing the detrimental effects of environmental change (Reed et al., 2011). However, phenotypic plasticity can also be costly (Chevin et al., 2010) and the adaptation to new environmental conditions may be limited by reaction norms, which evolved under different environmental conditions (Ghalambor et al., 2007). In the long-term, adaptive evolution may thus be essential for populations to cope with changes in environmental selection pressures (Bradshaw et al., 2006). It remains challenging to determine whether temporal changes in traits are the consequence of plasticity or adaptative evolution (P. Gienapp et al., 2008; Merilä & Hendry, 2014). Obtaining strong evidence of adaptive evolution requires obtaining information about the genetic basis of traits and demonstrating that selection has induced temporal genetic changes (Merilä & Hendry, 2014).

Salmon, including Atlantic salmon (*Salmo salar*) are economically, culturally and ecologically important species, considered to be indicators of ecosystem health (Jonsson & Jonsson, 2011; Pokki et al., 2018). Most Atlantic salmon are anadromous, with juveniles staying several years in river before smoltifying and migrating to feeding grounds at sea. They then spend a period of one to five years at sea (hereafter sea age or age at maturity) before maturing and returning with a high degree of fidelity to their natal river to spawn. A small proportion of individuals can survive, recondition and spawn again in subsequent years. Some males can mature in freshwater at the parr stage and reproduce before eventually starting their marine migration. This life cycle exposes Atlantic salmon to alterations of both freshwater and marine environments. Construction of dams, intensive aquaculture, climate change and overexploitation are some of the potential causes of the global decrease in Atlantic salmon abundance observed in the last decades (e.g. Gerald Chaput, 2012; Forseth et al., 2017; Parrish et al., 1998). Temporal variation in life history traits such as age at maturity has also been widely described (e.g. Jonsson et al. 2016; Niemelä et al. 2006; Otero et al. 2012) and may partly explain the observed decrease in salmon production (e.g. Bror Jonsson & Jonsson, 2004). Although several environmental variables have been associated with changes in life history traits, little is known about the proximate cause of such variation (i.e. non- or mal-adaptive changes resulting directly from a stressful environment or adaptive changes potentially favoring populations resilience; Crozier and Hutchings 2014).

Age at maturity in Atlantic salmon, or sea age, influences fitness, is heritable and can consequently evolve under natural selection. This trait represents a trade-off between survival and reproduction, whereby individuals spending more time at sea get bigger at the expense of higher risks of mortality before maturing. Adult size is positively correlated with breeding success in both sexes, but to a lesser extent in males (Fleming, 1998). Age at maturity has been strongly associated with a single locus in the *vgll3* region, explaining 40 percent of the variability observed in 54 populations from Northern Europe (Barson et al., 2015). This locus displays sex-specific effects with reversal dominance, which would have evolved to reduce sexual conflict (Barson et al., 2015). Temporal changes in environmental conditions can modify the benefits and/or cost of maturing at certain ages. Such natural or human-induced selection could direct the population age at maturity toward a new optimum by inducing temporal changes in *vgll3* allele frequency. Age at maturity thus provides a rare opportunity to study contemporary evolution by tracking changes simultaneously at the phenotypic and genetic levels.

Salmon from the Teno river located at the border between Finland and Norway (Figure 1) have been extensively monitored and studied, providing valuable knowledge and material for the study of evolution and population dynamics. Since 1972, fishers have collected scales from more than 154,000 salmon caught all over the Teno river system, along with information about individuals' sex, length and weight. Scales inform about life history traits of each individual (ICES 2011) and can be used for DNA extraction. Monitoring extends beyond the collection of scales by, for instance, counting adult salmon with snorkeling, video or recently sonar (e.g. Orell et al., 2011) or identifying the genetic stock of individuals caught at sea and in the river (Vähä et al., 2016). The presence of 28 genetically distinct and potentially locally adapted populations (Pritchard et al., 2018; Vähä et al., 2016) emphasizes the necessity to develop integrative models for population viability evaluation in this river.



Figure 1: Map of the Teno river located at the border between Finland and Norway.

From Erkinaro et al. 2019.

Aims of the thesis:

This thesis is organized around five different aims which consist of:

- 1 Characterizing the spatial and temporal variations in life history strategies in the Teno river, while accounting for confounding factors related to sampling (fishing gears, sampling size and period...) (**chapter I**)
- 2 Identifying the proximate cause of temporal changes in age at maturity in two focal populations with contrasting age structure: has age at maturity evolved during the last 40 years? (**chapter II, chapter III**)
- 3 Identifying the ultimate causes of changes in age at maturity with an ecosystem approach: what are the direct and indirect effects of human activities and environmental changes? (**chapter IV**)
- 4 Determining the potential consequences of sex-specific *vgll3* effects on selection and evolutionary response to selection (**chapter II**)
- 5 Developing an integrative population dynamics model for the Utsjoki river (**chapter IV**)

Materials and methods:

All chapters of this thesis make use of a long-term dataset obtained by the collection of Atlantic salmon scales and phenotypic information (i.e. length, weight and sex) by trained fishers in the Teno river. Scale reading, following international guidelines (ICES, 2011), allowed the determination of smolt age, sea age and number of breeding attempts for more than 154,000 individuals. The Teno river host large and diverse Atlantic salmon populations, exploited by tourist anglers and local fishers using different fishing methods (rod, weir, gillnet and driftnet fishing).

Describing life history variation

Chapter I aims at describing the temporal and spatial variation in life history diversity in the Teno river while accounting for differences in sampling effort, by using individual-based rarefaction and extrapolation curves and Hill number of order 1 (Chao et al., 2014; Hill, 1973). Temporal and spatial variations in the most frequent smolt age groups and in sea age (including previous spawners) were determined using respectively generalized additive models (GAM) and generalized linear models (GLM). Sex, fishing months and gears were included as independent variables in the sea age analyses.

Identifying the factors affecting temporal variations in age at maturity

Chapter II aims at determining whether age at maturity evolved between 1972 and 2014 in two populations from the Teno river that display a contrasting age at maturity structure. About 60 scales from the Teno mainstem and the Inarjoki river (Figure 1) were randomly selected per year in order to extract DNA. All scales were collected from salmon caught with a rod from the 20th of July to the 31st of August, when most of the salmon are expected to have reached their home spawning ground (Niemelä, Orell, et al., 2006). DNA extraction, sex determination and genotyping at 191 loci including *vgll3* were achieved following Aykanat et al. 2016. Individuals were assigned to the Tenojoki or Inarjoki population using the software STRUCTURE (Falush et al., 2003), with juveniles from both populations as baselines. Temporal trends in *vgll3* allele frequency were determined for each population with separate quasi-binomial GLM and compared with all other loci which had genotyping success > 0.70. The temporal trends in putatively neutral loci were used as a basis for calculating the amount of drift expected at *vgll3* under a Wright-Fisher model (Fisher, 1930; Wright, 1931), given the *vgll3* initial allele frequency. A Bayesian Wright-Fisher model was also used to estimate the selection coefficient necessary to induce the observed changes in *vgll3* allele frequency, assuming similar selection between males and females. The sex-specific effect of *vgll3* on age at maturity in each population was determined by using separate multinomial models. The year of capture was included as an independent variable and held fixed in the Tenojoki model in order to determine the sex-specific evolutionary responses to genotype frequency changes.

Chapter III aims at identifying the environmental drivers of *vgll3* allele and genotype frequency variation in the Tenojoki population. The genetic data described above was used. The individual *vgll3* allele frequency was regressed in a quasi-binomial model with the following included as independent variables: sea temperature, log biomass indices of salmon prey in the Barents Sea (krill, capelin and herring), number of nets at sea (i.e. in Finnmark), net fishing licenses in the river and tourist rod fishing license-days. A multi-species Gompertz model developed by Langangen et al. 2017 was used to estimate the effect of fishing on capelin log biomass, while accounting for density dependence, interactions

between key species of the Barents Sea and temperature effects. The Monte Carlo method for assessing mediation (MacKinnon et al., 2004) was then used to estimate the indirect effect of capelin harvesting on *vgll3* allele frequency. A post-hoc analysis using sonar data from 2018 was performed to estimate the selectivity of three different net fishing methods (weir, driftnet and gillnet) in the Teno mainstem and how changes in the relative use of each gear may influence the direction and magnitude of selection on *vgll3*.

Developing a Bayesian integrative life cycle model in Utsjoki

Chapter IV aims at developing a Bayesian integrative life cycle model in Utsjoki, located in the lower part of the Teno river system (Figure 1). Utsjoki is one of the largest tributaries of the Teno river with 1665 square kilometers of catchment area. Summer migrating smolts and adults were counted using video cameras set up at the entry of the river from 2002 to 2014. In some years, Utsjoki individuals were identified from mixed stock fisheries catches using microsatellite markers. Consequently, this river represents a data-rich case and is a good starting point to develop a Bayesian life cycle model which can be extended in the future to the whole Teno river system. Indeed, Bayesian hierarchical models permit the transfer of information from data-rich to data-poor cases, allowing learning from e.g. different years or stocks (Kuparinen et al., 2012; Punt et al., 2011). Bayesian modelling also allows the incorporation of various sources of information by using prior distributions. In this study, for instance, we introduced into the model expert knowledge about the carrying capacity of the Utsjoki river, and a prior distribution for egg maximum survival derived from a meta-analysis that included nine other Atlantic salmon stocks (Pulkkinen & Mäntyniemi, 2013). Bayesian models can also account for different sources of uncertainty, e.g. observation errors or process errors arising from environmental or dynamic stochasticity, which will be propagated into the different parts of the model. A drawback of Bayesian methods is the demanding computing required to reach convergence. Measurement models may be sometimes too complex to be directly integrated into the full life cycle model. Instead, the measurement model can be run separately and the likelihood function can be approximated inside the life cycle model (e.g. Michielsens et al., 2008). For instance, the annual number of smolts migrating out of the Utsjoki river was first estimated from video counts, using a Bayesian arrival model powered by expert knowledge and environmental variables (Pulkkinen et al. 2018, submitted). The estimated annual number of smolts was then included in this study using likelihood approximation.

Results and discussion

Important life history diversity and variability in the Teno river system (chapter I)

A total of 120 different life history strategies (i.e. combinations of life history traits) were observed in the Teno river between 1975 and 2014, with a high diversity in smolt age (2-8 years), sea age (1-5 years) and forms of alternate and consecutive spawners (representing 54 and 37 combinations, respectively). This is one of the largest number of life history strategies described in a single river, despite an important diversity also observed in Canadian rivers (e.g. smolt age 1-7 years, sea age 1-4 years, Chaput et al., 2006). Nevertheless, most of those strategies were rare (Fig. 2) and unlikely to influence the dynamics of populations. Overall, diversity in life history strategies may reduce the deleterious effects on populations of localized and/or short-term variations in environmental conditions, by spreading risks via the portfolio effect (e.g. Schindler et al., 2010). The number of life history combinations varied greatly among locations and also temporally, by being related to changes in proportions of previous spawners.

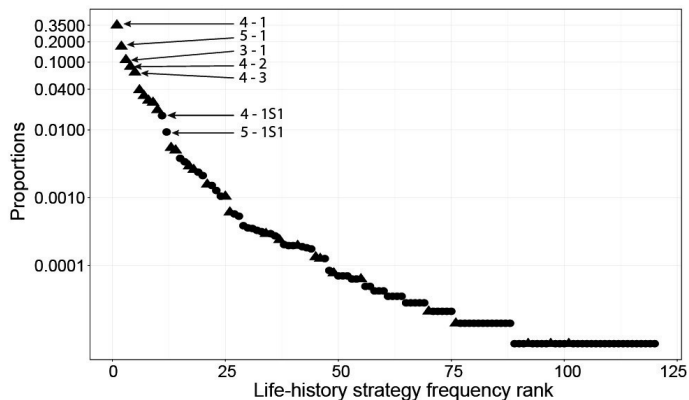


Figure 2: Proportion in Teno Atlantic salmon catches of the different life history strategies (smolt age – sea age) ranked by their frequency.

In most locations, the proportion of previous spawners and individuals maturing after two years at sea (2 sea winter, 2SW) increased during the 40-year period whereas the proportion of individuals maturing after one (1SW) and particularly after three years at sea (3SW, slope (odds) = 0.970, $CI_{95} = [0.965, 0.974]$) declined (Fig. 3). The trend in female 1SW in the Teno mainstem was positive and thus different from other rivers. This could be explained by an increase in the contribution of early maturing individuals from small tributaries in the mainstem mixed-stock catches. Indeed, the genetic assignments in **chapter II** revealed that the proportion of 1SW female in the mainstem population, Tenojoki, is low (< 5%). Consequently, it appears more appropriate to investigate drivers of life history trait variation in individuals with a genetically determined population of origin (e.g. Tenojoki in **chapter III**). The proportion of the different age at maturity classes (1-3SW) and previous spawners also differed spatially, particularly in females, inducing spatial variation in the degree of sexual dimorphism (Figure 3).

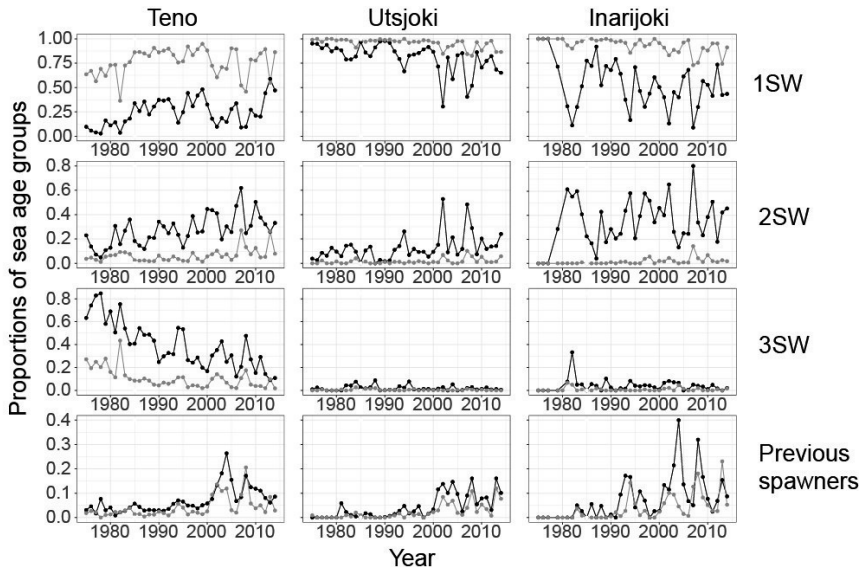


Figure 3: Temporal variation in the proportion of 1-3SW and previous spawners in the Teno mainstem and two tributaries, Utsjoki and Inarijoki.

Males are in black and females in grey.

Fisheries induced evolution of age at maturity in Tenojoki (chapter II and III)

In **chapter II**, we investigated whether age at maturity evolved under selection between 1975 and 2014 in two populations with contrasting age structure, Tenojoki and Inarijoki. We found clear evidence for temporal changes in age at maturity and in allele frequency of *vgll3*, the locus associated with age at maturity (Figure 8a, Barson et al. 2015), in Tenojoki only. The mean age at maturity declined by more than 40% in males (from 2.2 to 1.3 years), particularly during the first 17 hatch years (GAM effective degrees of freedom (EDF) = 3.87, $F = 5.11$, $P < 0.001$), and 8% in females (from 3.0 to 2.7 years), in a slightly non-linear way (EDF = 1.27, $F = 0.57$, $P = 0.02$; Figure 4a). The *vgll3* late maturation allele frequency (called *vgll3***L* hereafter) declined by 18% during the same period and was the largest change observed among the 144 genome-wide single-nucleotide polymorphisms (SNPs) assessed (Figure 4b). Drift was unlikely to be the main driver of *vgll3***L* allele frequency decline ($P_{\Delta_{vgll3}} = 0.004$ or 0.022 after accounting for sampling variance; estimated based on other loci by normal approximation of a Wright–Fisher model). Evolution of *vgll3* allele frequency was also unlikely to be the consequence of changes in migration patterns as migration rates among populations of the Teno river are low and temporally stable (Vähä et al., 2008). These results thus provide evidence of rapid adaptive evolution of age at maturity toward small, early maturing individuals. Over time, the cost of late maturation may have become too large to be compensated by the reproductive advantage provided by a larger body size. The potential drivers of age at maturity evolution in Tenojoki were investigated in **chapter III**.

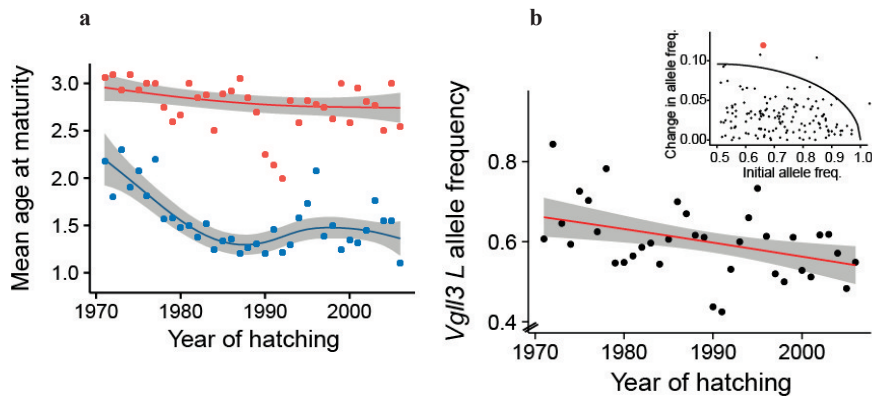


Figure 4: Temporal variation in a) mean age at maturity in males (blue) and females (red) and b) *vgll3*L* allele frequency over 36 hatch years in Tenjoki.**

Lines represent the model fitted values from the a) GAM b) quasi-binomial GLM and the shaded area ± 1.96 standard error. Insets display the absolute temporal change in allele frequency estimated from quasi-binomial models for 144 loci with genotyping success greater than 0.7. The *vgll3* locus is in red. The line represents the calculated amount of drift under a Wright-Fisher model at the 97.5 quantile.

The environment for Tenjoki Atlantic salmon has changed over the last forty years, in term of annual temperature of the Barents Sea (Tereshchenko, 1996), riverine and sea fishing intensities (e.g. Jensen et al., 1999) and biomass of major prey species such as krill, capelin and herring (ICES, 2015, 2017). All of these variables were included as predictors of *vgll3* allele frequency in a quasi-binomial GLM. Results indicated that the number of riverine net fishing licenses, corrected for the number of fishing days allowed per week, and the log biomass of capelin were positively associated with the late maturation allele ($F_{(1)} = 27.79$, $P < 0.001$ and $F_{(1)} = 20.77$, $P < 0.001$, respectively; Figure 5 and Figure 6). Those variables remained significant in the model with de-trended predictors and the year effect included ($F_{(1)} = 14.15$, $P < 0.001$ and $F_{(1)} = 10.64$, $P = 0.001$, respectively; Figure 5), indicating that both variables explained variation in *vgll3* allele frequency around the long-term temporal trend (Grosbois et al., 2008). The biomasses of other prey species, krill and herring, were also positively associated with *vgll3***L* ($F_{(1)} = 6.42$, $P = 0.011$ and $F_{(1)} = 9.30$, $P = 0.002$, respectively; Figure 5) but not anymore in the de-trended model ($F_{(1)} = 2.05$, $P = 0.153$ and $F_{(1)} = 3.23$, $P = 0.072$, respectively; Figure 5).

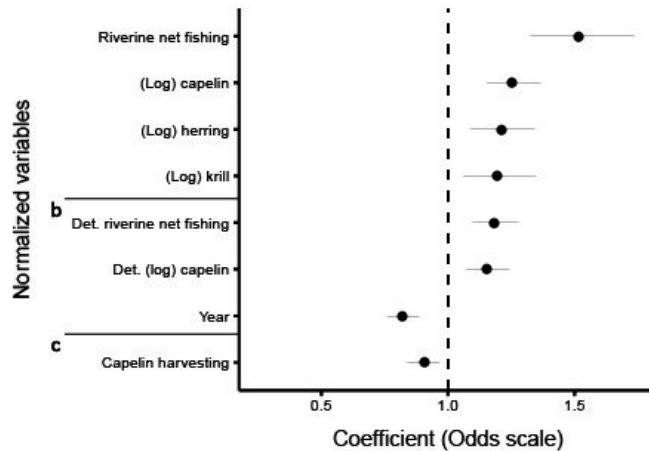


Figure 5: Standardized effect of significant variables on *vgll3*L* odds.**

Estimates come from the **a)** initial quasi-binomial model, **b)** de-trended (det.) model and **c)** Monte Carlo Method for Assessing Mediation. The dotted line indicates no effect on *vgll3* odds. The error bars correspond to 95% confidence intervals.

The capelin stock of the Barents Sea has experienced three different collapses over the last 40 years which have been partly attributed to fishing (Hjermann et al., 2004). We used a multispecies Gompertz model developed in Langanen et al. 2017 to estimate the effect of fishing on capelin log biomass while accounting for density dependence and ecosystem interactions. The Monte Carlo Method for Assessing Mediation (MCMAM) (MacKinnon et al., 2004) then allowed us to detect a significant 30% decrease in *vgll3***L* allele odds per harvest unit ($CI_{95\%} = [0.116, 0.471]$; Figure 5 and Figure 6), while accounting for uncertainty in estimates. This negative effect was likely stronger during the first 15 hatch years, when most of the evolutionary changes occurred. Although indirect ecological effects of fishing are often recognized (Heino et al., 2015; e.g. Naylor et al., 2000), evidence for indirect evolutionary effects has not previously been found (Heino et al., 2015).

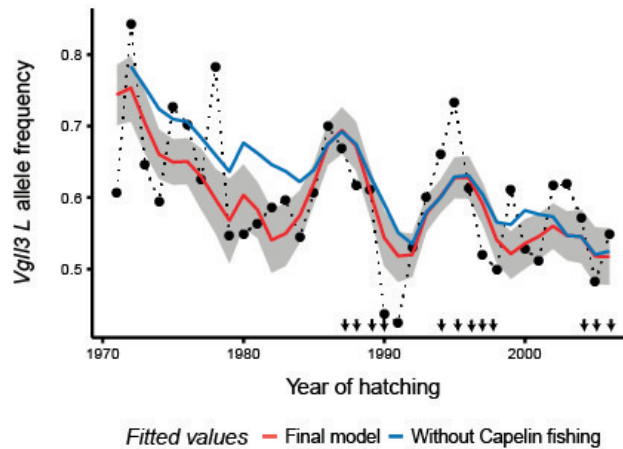


Figure 6: Temporal changes in *vgll3*L* allele frequency in Tenojoki and expected effect of capelin harvesting.**

The black dotted line represents the observed data and the red line the averaged fitted values from the quasi-binomial model including environmental variables as predictors. The shaded area corresponds to bias-corrected and accelerated (BCa) 95% bootstrap intervals based on 3000 replicates. The blue line represents the indirect effect of capelin harvesting estimated by fixing fishing at zero in the multispecies Gompertz model. Arrows indicate capelin fisheries closure following collapses or low harvest rate (estimated harvest rate < 0.5%).

Traditional net fishing in the Teno mainstem includes the use of weir, gillnet and driftnet. The positive effect of riverine net fishing effort on the *vgll3***L* allele frequency may be explained by the predominant use of weirs (54% of net catches on average), selecting mainly small individuals. Indeed, sonar data from 2018 indicated that weir fishing select against the early maturation *vgll3***E* allele by capturing proportionally more small individuals, whereas driftnet and gillnet select against the *vgll3***L* allele, with some differences in the strength of selection among sexes. Globally, riverine net fishing was expected to be selective against the *vgll3***E* allele in the early years of the time series (Figure 7), when the fishing effort decreased, likely accelerating the decline in *vgll3* late maturation allele initially induced by other factors (e.g. prey biomass). Those calculations assumed identical gear selectivity and *vgll3* effect among years but accounted for temporal variation in female proportion and in the relative use of each net fishing method. Socio-economic pressures may be too strong in certain situations to allow consequent reductions of fishing harvest rates to control fisheries induced evolution (Hard et al., 2008). In the Teno river for instance, fishing is part of the Sami's constitutional right to practice their culture. As an alternative, selection pressures exerted on the different ages at maturity by net fishing might be controlled by modifying the relative use of the different gears. However, this requires beforehand a further collection of data (e.g. multiple years of genetic stock assignment and sonar counting) and the development of more advanced models that couple population dynamics and evolutionary genetics (Reed et al., 2011). Indeed,

selection patterns may be complex and differ between the sexes and among populations (e.g. Kuparinen & Hutchings, 2016) as, for instance, a consequence of variation in genetic architecture (see below).

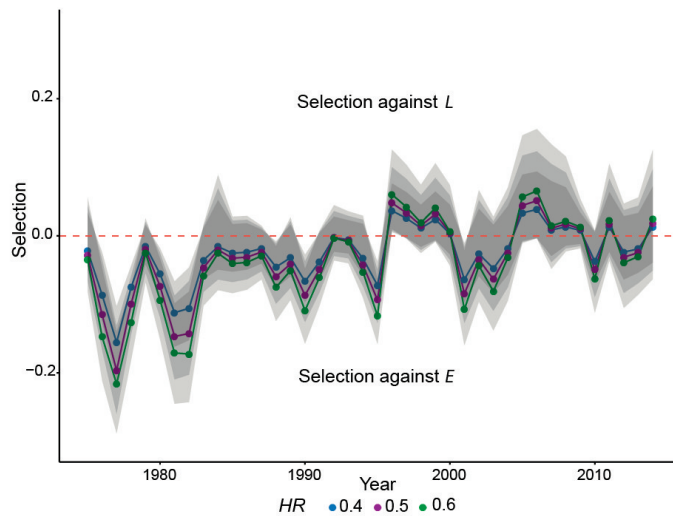


Figure 7: Estimated temporal variation in riverine net fishing selection as a function of the harvest rate.

Estimates are based on length dependent capture probabilities of salmon for 3 different gears (inferred from sonar data in 2018), on sex-specific *vgll3* association with length and on temporal variation in females proportion and the relative use of the different fishing gears.

Population- and sex-specific *vgll3* effects: consequences on selection and evolutionary response (chapter II)

The Inarijoki and Tenojoki populations, although being genetically similar (genetic differentiation $F_{ST} = 0.013$), displayed contrasting age at maturity, *vgll3* allele frequencies and genetic architectures (Figure 8). The probability to observe the different ages at maturity varied in a sex-specific manner according to the *vgll3* genotypes in Tenojoki (multinomial model including a year effect, $\chi^2_{(6)} = 27.58$, $P < 0.001$). In Inarijoki, *vgll3* was also significantly associated with the probability of observing the different ages at maturity ($\chi^2_{(4)} = 56.41$, $P < 0.001$) but not in a sex-specific manner ($\chi^2_{(4)} = 8.27$, $P = 0.08$). Mean age at maturity per genotype was then calculated from the model fitted values. The relative difference in mean age at maturity (i.e. additive effect) varied depending on the sex and population. In Tenojoki, the relative difference in age at maturity between homozygotes *EE* and *LL* was about three times higher in males (+106% for *LL*, +1.17 years, $CI_{95} = [0.99, 1.33]$) than in females (+32% for *LL*, +0.71 years, $CI_{95} = [0.51, 0.91]$; Figure 8a). In comparison, the relative difference in age at maturity between homozygotes in Inarijoki was about six times larger in females (+74% for *LL*, +0.94 years, $CI_{95} = [0.68, 1.25]$) than

in males (+12% for *LL*, +0.13 years, $CI_{95} = [0.05, 0.22]$, Figure 8b). Given that survival at sea is dependent on the migration duration, selection at sea (i.e. the difference in relative fitness between homozygotes) is expected to be larger in males in Tenojoki and in females in Inarjoki. This was supported by the sex-specific allele frequency patterns observed in each population. Tenojoki males had on average lower *vgll3* late maturation allele frequency than females when returning to the river ($F_{(1)} = 8.72$, $P < 0.01$). Inversely, Inarjoki males had on average higher *vgll3***L* allele frequency than females ($F_{(1)} = 36.51$, $P < 0.001$). No differences were detected at the juvenile stage in both populations ($\chi^2_{(1)} = 3.27$, $P = 0.07$ in Tenojoki, $\chi^2_{(1)} = 0.04$, $P = 0.85$ in Inarjoki). Genetic architecture is thus likely to influence sex-specific strength of selection during salmon migration.

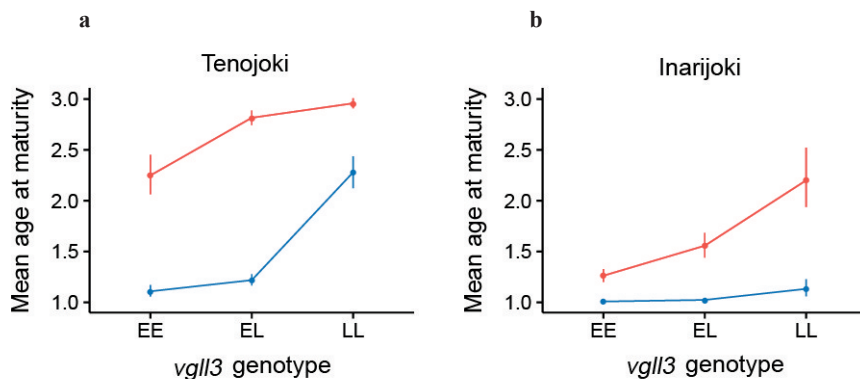


Figure 8: Mean age at maturity as a function of *vgll3* genotype in the a) Tenojoki and b) Inarjoki populations.

Females are in red (N Tenojoki = 522, N Inarjoki = 286) and males in blue (N Tenojoki = 804, N Inarjoki = 612). Means are calculated from multinomial models fitted values, averaged over years. Error bars represent 95% bootstrap confidence intervals based on 1000 replicates.

Genetic architecture also influenced the sex-specific evolutionary response to selection. At each reproductive event, the genetic pools of males and females are mixed. As a consequence, we detected no significant difference in temporal variation of *vgll3* genotype frequencies in Tenojoki (multinomial model, $\chi^2_{(2)} = 2.78$, $P = 0.25$). However, temporal variation in age at maturity differed between sexes (Figure 4a), partially because of variations in the evolutionary response. We found that changes in genotype frequency did not induce any clear trend in female age at maturity (0 year, GAM EDF = 0, $F = 0$, $P = 0.54$) but was responsible of about 50% of the non-linear decrease in male age (0.46 years, GAM EDF = 3.95, $F = 3.51$, $P < 0.001$). Differences in sex-specific additive and dominance effects are expected to be one of the drivers behind such contrasts in sex-specific evolutionary responses. These results highlight the importance of knowing the genetic basis of fitness traits in order to better understand their evolution (e.g. Kuarinen & Hutchings, 2016, 2019) and explain the phenotypic diversity observed among species and populations. They also highlight the difficulties in managing populations from the same river that potentially respond differently to environmental changes. Development of river- or stock-

specific population dynamics models are thus needed to improve our knowledge about the variation in abundance and composition of populations and factors affecting it.

Integrated Bayesian life cycle model (chapter IV)

Our Bayesian life cycle model revealed large temporal variation in the abundance of the different sea age groups in Utsjoki, with a marked increase in the number of large individuals after 2007 (Figure 9). This can partially be explained by a release of the fishing pressure on these individuals at sea and in the river. Natural survival during the first year at sea (0.13-0.60) and to the next breeding attempt (0.21) were large in comparison with values previously reported in literature (e.g. Jonsson et al., 1991; Michielsens et al., 2006). The number of smolts often deviated from expected numbers calculated with a Beverton-Holt model, likely because of environmental stochasticity (Figure 10). Probabilities to attain management reference points were about 50% lower when calculated using the realized number of smolts, i.e. after accounting for variations in recruitment. The extension of this Bayesian model to other stocks with similar age structure and migration pattern may provide additional information for parameters such as survival after the first year at sea, quite uncertain currently. Increase in model complexity may be handle by using faster MCMC samplers as a result of recent package and software development (e.g. Monnahan & Kristensen, 2018).

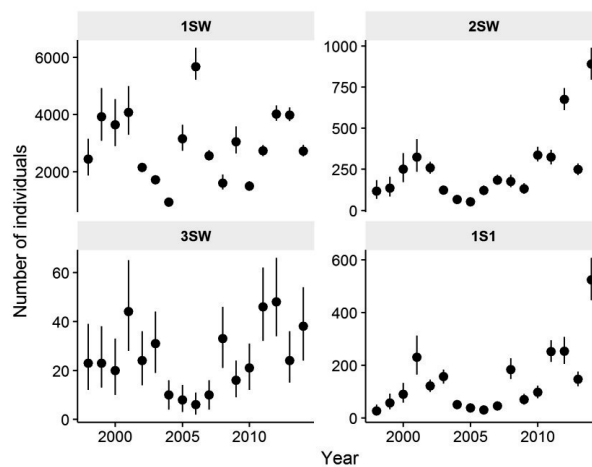


Figure 9: Temporal variation in the abundance of spawners from different age groups.

Dots represent the model posterior medians. Error bars represent 95% credibility intervals based on 6000 samples. 1S1 refers to previous spawners maturing after one year at sea, remaining one year in river to spawn and one year at sea to recondition.

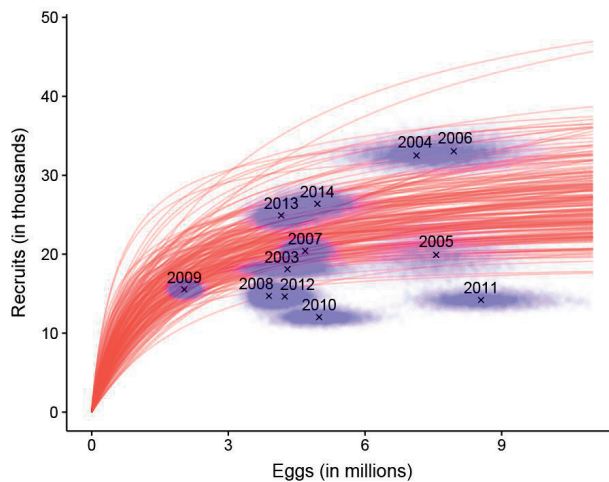


Figure 10: Stock-recruitment relationship in Utsjoki.

Red lines were randomly drawn from the posterior distribution and represent the uncertainty in the stock-recruitment relationship median (200 samples). Numbers are years of smoltification. Purple dots represent the uncertainty in the eggs-smolts historical pairs (6000 samples).

Limitations and perspectives

The results presented in this thesis improve our knowledge about the evolutionary dynamic of age at maturity in the Teno river and the factors potentially influencing it. However, important questions remain, particularly about the sex-specific optimal age at maturity or *vgll3* genotype, once survival and reproduction are accounted for. We showed that the *vgll3* sex-specific additive and dominance effects in Tenojoki likely limited an evolutionary response in females, while favouring an evolutionary response in males. Such responses could be favorable in presence of sexually antagonistic selection (whereby males are selected for maturing early and females late), conditions under which the sex-specific *vgll3* effects would have evolved to reduce sexual conflict (Barson et al., 2015). However, quick changes in environmental conditions may also have modified the nature of selection, from sexually antagonistic selection to directional selection in favor of early maturing individuals in both sexes (e.g. Connallon & Hall, 2016). The development of a population dynamics model, which could later be coupled with an evolutionary model, is a first step towards a better understanding of sex-specific selection in the Teno. This would also require further genetic studies, by creating for instance pedigrees (e.g. Mobley et al., 2019) to better understand the relationship between *vgll3* genotypes and reproductive success, or studying in more details the potential pleiotropic effects of *vgll3*, which may affect sex-specific selection.

Recent studies have indicated that *vgll3* could have pleiotropic effects or be close in the genome to other loci affecting male parr maturation (Lepais et al., 2017) and iteroparity (Aykanat et al., 2019). It is thus possible that temporal changes in those traits may affect *vgll3* dynamics, by either constraining evolution or speeding it up (Phillip Gienapp & Brommer, 2014). Maturation at the parr stage represents a rare alternative strategy for males in the subarctic Teno river (typically 10%, Heinimaa and Erkinaro 2004), compared to more southern salmon populations. Consequently, although selection acting on this trait could have contributed to the observed evolution of *vgll3* allele frequency, selection acting on sea age at maturity is expected to be a more important driver. Moreover, the effect size of the parr maturation QTL identified on chromosome 25, explaining 20.6% of variation in the maturation size threshold in a semi-natural environment, could be considered low in comparison to the effect of *vgll3* on age at maturity in some populations. In addition, Lepais et al. 2017 advised further investigation to refine the early male maturation genomic architecture, as there is currently no direct evidence that *vgll3* is the causative locus. Aykanat et al. 2019 showed that the odds ratio of survival until the next breeding attempt were 2.4 times higher with the *vgll3*EE* genotype than with *vgll3*LL*, even if it remained unclear whether *vgll3* controls both iteroparity and age at maturity. The increase in proportion of repeat spawners in the Teno river (**chapter I**, Niemelä, Erkinaro, et al. 2006), and potentially in the mainstem Tenjoki population, may have contributed to the decrease in the observed *vgll3*L* allele frequency. However, only 2.7% of the Tenjoki individuals in **chapter II** and **III** were previous spawners. This suggests that the increasing percentage observed in the mainstem may be due to contribution of other populations and that the influence of iteroparity on Tenjoki *vgll3* allele frequency dynamics may be limited. Further studies are needed to evaluate the temporal changes in previous spawner proportions in this population.

Obtaining empirical evidence of fisheries induced evolution in wild populations is challenging (Hard et al., 2008). We found a significant association between the number of riverine net fishing licenses and *vgll3* allele frequency variation and further determined, using sonar data from 2018, that the most used fishing method was likely to be selective against *vgll3*E*. We then estimated the expected selection over time by assuming identical gear selectivity and accounting for female proportion and for changes in the relative use of each fishing method. There is however a need to estimate more precisely the selectivity of different fishing gears for the different populations of the Teno river, which may differ in their age structure, age at maturity genetic architecture and migration timing (**chapter I**, **chapter II**, J.-P. Vähä et al. 2011). This could be done by coupling sonar data, catch data and genetic stock identification over several years. The use of an eco-evolutionary dynamics model that integrates data about gear selectivity, harvest rate and age at maturity genetic architecture would help us in determining selection induced, for instance, by the constant size selective removal of individuals, which could not be detected using simple regressions. Consequently, we cannot exclude the possibility for fisheries not significantly associated with *vgll3* allele frequency changes in **chapter III** to induce evolutionary changes in age at maturity. In that sense, our work should constitute a premise for further investigations. Eco-evolutionary dynamics models would also constitute a useful tool to improve our understanding of the interaction between ecology and evolution and its consequences for population viability.

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