Migration in Anadromous Brown Trout

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Opponent är Dr. Martyn Lucas, School of Biological and Biomedical Sciences, Durham University, UK

Cover illustration: Adult sea trout (Erik Kohlström, http://erikkohlstrom.se/)

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To Cecilia

Abstract

This thesis investigates the anadromous migration of brown trout (*Salmo trutta*) with the overall aim to improve stock management within the region. Several field studies were conducted in different streams and coastal areas on the west coast of Sweden specifically aimed to evaluate environmental triggers for migration (**Paper I**), migration pathways and strategies (**Paper III and IV**) as well as the genetic differentiation of anadromous populations of brown trout (**Paper V**). In order to evaluate the effect of increasing air temperatures on sizes and abundances of different year classes (**Paper II**), observational data from the Swedish electrofishing database and scientific reports were used.

These studies show that downstream migration is triggered both by discharge and temperature, but that these environmental cues may act differently between years (**Paper I**). Downstream migration was found to be primarily nocturnal in the river and in the estuary, often occurring in mixed species shoals (**Paper I and III**). The downstream migration was observed to occur in two main clusters, one early and one late migration group (**Paper IV**). The level of discharge was also found to affect mortality rates, where lower discharge caused increased mortality (**Paper III**). Migration speed decreased further out from the river, probably reflecting an initial navigation phase towards the sea followed by a subsequent foraging phase in the sea (**Paper III and IV**). When investigating the genetic differentiation on the west coast of Sweden we found four distinct genetic clusters in the rivers, whereas a total of nine genetically different clusters where present in the sea on the Swedish west coast (**Paper V**). The analysis of data from the Swedish electrofishing database SERS revealed that recruitment has remained constant over the last 30 years, whereas the density of older cohorts has decreased. However, the size of the individuals in the young-of-the-year cohort has increased whereas the size of smolts has decreased over the same period indicating that the proportion of brown trout parr that smoltify and migrate to the sea as 1yr smolts has increased (**Paper II**).

My results indicate a large variation in migration tactics between years, rivers, as well as within rivers (**Paper I, III and IV**). This variation makes it difficult to establish general conservation measures and regulations for threatened populations in certain rivers. On the other hand most rivers contain sea trout that belong to a larger genetic cluster, with seemingly little or no local adaptation (**Paper V**). Consequently, management actions and conservation measures should be adopted for each specific genetic cluster, and only for individual rivers when large survival bottle necks (e.g. weirs, dams and wetlands) are identified

KEYWORDS: Downstream migration, temperature, discharge, genetics, growth rate, climate change, *Salmo trutta*, *Salmo salar*, sea trout, salmon

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Populärvetenskaplig sammanfattning

I den här avhandlingen undersöks havsöringens (*Salmo trutta*) vandring ut i havet. Det övergripande målet med avhandlingen är att använda resultaten för att förbättra beståndsförvaltningen i området. Flera fältstudier genomfördes i olika vattendrag och kustområden längs med den svenska västkusten för att utvärdera vilka faktorer som påverkar: smoltutvandringen (**Artikel I**); vandringsvägar i havet och vandringsstrategier (**Artikel III och IV**), samt för att undersöka den genetiska skillnaden mellan västkustens havsöringspopulationer (**Artikel V**). För att utvärdera effekten av regional uppvärmning (lufttemperatur) på storlek och förekomst av olika årsklasser av öring (**Artikel II**) användes data från den svenska elfiskedatabasen (SERS) tillsammans med olika vetenskapliga och statliga rapporter.

Studierna visar att nedströms vandring utlöses av både ökat vattenflöde och temperatur, men att dessa två faktorer kan påverkar vandringen i varierande utsträckning mellan år (**Artikel I**). Vandringen nedströms sker framförallt på natten i ån och i mynningsområdet, oftast i stim tillsammans med andra arter (**Artikel I och III**). Vandringen är uppdelad i en tidig och en sen grupp (**Artikel IV**). Vattenflödet i ån visade sig påverka dödligheten, där ett lågt flöde ökade dödligheten hos den vandrande fisken förmodligen för att de lättare upptäcktes av rovdjur (**Artikel III**). Havsöringens simhastighet minskade ju längre ut i havet från ån de kom, troligen för att de till en början försöker navigera sig ut mot havet för att sedan stanna upp och leta efter föda (**Artikel III och IV**). Den genetiska undersökningen visade att det finns fyra olika genetiskt distinkta populationer i åarna på västkusten, men att totalt nio stycken förekom i havet (**Artikel V**). Analysen av elfiskedata från SERS visade att antalet årsungar inte hade ändrat sig under de senaste 30 åren, medan tätheten av äldre ungar hade minskat (**Artikel II**). Det visade sig dock att storleken på årsungarna hade ökat medan storleken på de utvandrande individerna hade minskat under samma period. Detta tyder på att andelen av öringsungar som vandrar ut i havet efter ett år i ån har ökat (**Artikel II**).

Mina resultat visar att det finns en stor variation i havsöringens vandringstaktik mellan år, åar, samt inom en å (**Artikel I, III och IV**). Denna variation gör det svårt att lägga fram generella bevarandeåtgärder och regler för hotade havsöringspopulationer. Å andra sidan så visar den genetiska undersökningen att de flesta vattendrag innehåller öring som tillhör en större genetisk grupp med till synes väldigt liten eller ingen lokal anpassning (**Artikel V**). Följaktligen bör förvaltningsåtgärder och bevarandeåtgärder i stället antas för varje specifik genetisk grupp, och bara för enskilda år där man har identifierat en hög dödlighet som orsakas av t.ex. dammar och våtmarker.

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The author tagging a sea trout (Paper III)

Photo: Johan Höjesjö

Supervisor:	Assoc. Prof. Johan Höjesjö, Department of Biological and Environmental Sciences
Co-supervisor:	Prof. Jörgen I. Johnsson, Department of Biological and Environmental Sciences
Examiner:	Prof. Charlotta Kvarnemo, Department of Biological and Environmental Sciences

”Så nästa gång du fiskar öring: sprätta upp magarna på alla fiskar du fångat. Då kommer du bli förvånad eller förbryllad eller säga ”Aha” eller ”Var det inte det jag trodde!” I vart fall gör det fisket intressantare”

Gunnar Svärdson (1985)

List of papers

Paper I Aldvén, D., Degerman, E. & Höjesjö, J. 2015. Environmental cues and downstream migration of anadromous brown trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*) smolts. *Boreal Environmental Research*, **20**, 35–44.

Paper II Aldvén, D., Degerman, E., Aarestrup, K. & Höjesjö, J. 2016. Effect of increasing temperatures on growth and densities of anadromous brown trout (*Salmo trutta L.*) parr and smolts. *Manuscript*.

Paper III Aldvén, D., Hedger, R., Økland, F., Rivinoja, P. & Höjesjö, J. 2015. Migration speed, routes, and mortality rates of anadromous brown trout S*almo trutta* during outward migration through a complex coastal habitat. *Marine Ecology Progress Series*, **541**, 151–163.

Paper IV Aldvén, D., Závorka, L., Aarestrup, K. & Höjesjö, J. 2016. Migration pathways in a fjord of two populations of sea trout (*Salmo trutta L.*) smolts. *Submitted manuscript (Proceedings of the Second International Sea Trout Symposium, Dundalk, 2015)*.

Paper V Höjesjö, J., Aldvén, D., Lien, S., Kent, M., & Hansen, M.M. 2016. Genetic population structure of anadromous brown trout along the Swedish west coast. *Manuscrip*.

Contents

Definitions

Parr: A juvenile salmonid

Sea trout: The anadromous form of brown trout

Smolt: Here defined as a parr that has undergone morphological, behavioural and physiological changes that enables them to migrate into a saline environment still residing in freshwater

Post-smolt: A smolt that has entered sea water

Finnock: Small sea trout in their first year after smolt migration

Kelt: A sea trout after spawning before they return the sea

Veteran migrant: A sea trout that have completed a migration cycle from the river and back, including both kelts as well as non-spawning individuals


SAS
Sea trout at Sea

Introduction

In this thesis I will focus on migration in anadromous brown trout (Fig. 1); with a primary focus on the downstream migration of kelts and smolts from the river and into the sea, as well as the initial sea migration (estuary and coastline) on the west coast of Sweden (Fig. 2). By investigating which environmental cues that triggered downstream migration as well as river and sea migration patterns I aimed to increase the knowledge of sea trout migration. By combining this knowledge with information of the genetic differentiation on the west coast of Sweden I more specifically aimed to incorporate this combined information to establish sustainable management of the sea trout stocks on the west coast of Sweden.

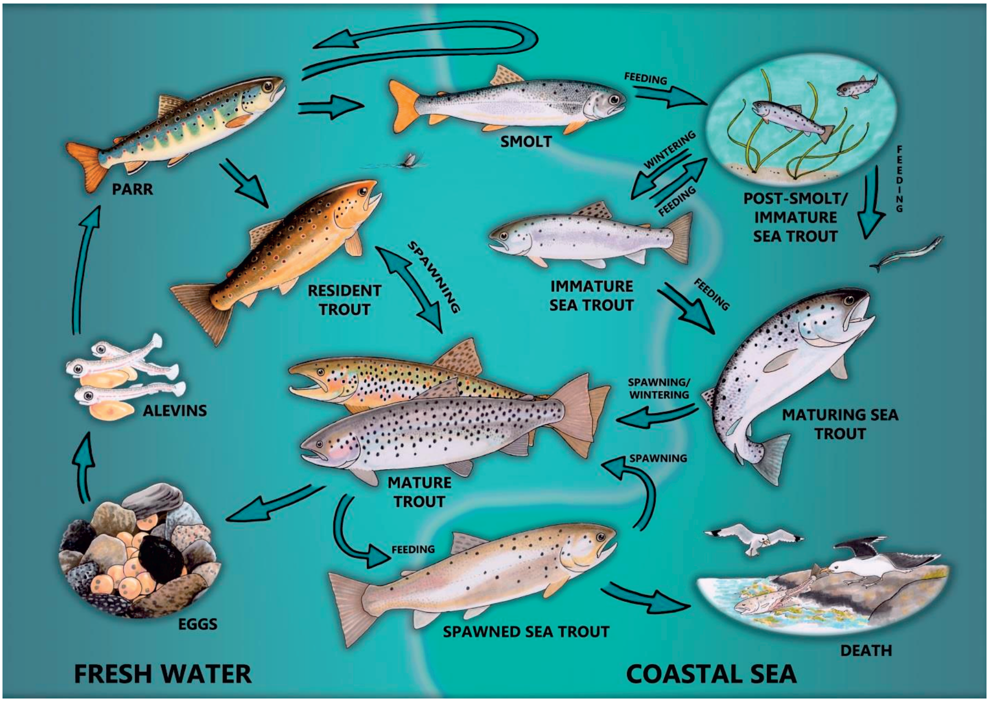

Figure 1: The sea trout (*Salmo trutta*) life-cycle (illustration by E. Kohlström).

Migration

Migration is often thought of as large scale movements such as the ungulate migrations on the African savanna (Wilmshurst et al. 1999), passerine bird migration to Africa (Biebach et al. 1986) or the upstream movement of Pacific salmon in North America (Schindler et al. 2003). However, migration is much more diverse, including all major branches of the animal kingdom (Dingle and Drake 2007). Migration is not a uniform pattern of movement but differs between populations of a species, but also between species, and the spatial space in which migration occurs can vary between a couple of km to several thousands of km as seen in e.g. Western sandpiper *Calidris mauri* and brown trout *Salmo trutta* (Berg and Berg 1987, O'Hara et al. 2005, Bartel et al. 2010). Migration in its true form is often defined as the movement of an entire population. However, with the exception of a few bird species (e.g. *Sterna paradisaea* and *Chen caerulescens*) most migratory populations experience a proportion of individuals that stay (Chapman et al. 2011). This phenomenon when both resident and migratory individuals are present within a population is called partial migration (but is often referred to as just migration). Here I will adopt a definition of migration as *the movement of a whole or parts of a population, from one area to another and back again which will include partial migration*. I will however not include movements that occur on a daily basis e.g. commuting or diel vertical migration (Dingle and Drake 2007).

Migration is believed to be a response to adverse conditions in the local environment (Taylor and Taylor 1977), as seen in the great migrations of the Serengeti (Wilmshurst et al. 1999), and in the winter migration of birds (O'Reilly and Wingfield 1995). The level of adversity in the habitat that causes the animal to migrate is governed by a trade-off between cost and benefits acting on the individual level (Northcote 1978, Gross et al. 1988), where the overall benefits of either strategy is increased reproductive success for the individual. However, the benefit in reproductive success for the individual is dependent on several factors, e.g. size and age etc. (Magnhagen and Kvarnemo 1989, Wooller et al. 1990). Therefore, migration can be segregated within the population as seen in salmonid species (Klemetsen et al. 2003). In salmonids, younger year classes often remain resident as the cost of migration becomes too high compared to the potential gain in reproductive success (Økland et al. 1993). In some species the locations and distance of migration may differ between sexes (van Eerden and Munsterman 1995, Jenkins and Cristol 2002, Komar et al. 2005, Nebel and Ydenberg 2005, Palacin et al. 2009). In cormorants *Phalacrocorax carbo sinensis*, for example the differences in migration distance can be a couple of hundreds of kilometers, were males generally overwinter closer to the breeding grounds compared to females that migrate further south (van Eerden and Munsterman 1995). The under lying causes for such differentiation is believed to depend on differences in mortality risk, reproductive cost, or physiological tolerance towards salt water (Jonsson et al. 2001, Nebel and Ydenberg 2005, Palacin et al. 2009). The differences in migration strategy within populations, i.e. why some stay and some migrate, have led to a variety of general hypotheses (Belthoff and Gauthreaux 1991, Chapman et al. 2011). First, the body size hypothesis states that resident individuals are larger as they are better at competing for resources such as nest sites and drifting food items (Chapman et al. 2011). According to this hypothesis smaller individuals should migrate as they are poorer at competing for recourses and less suitable for winter conditions (where the actual cost refers to thermal tolerance and fasting endurance). This may hold for some birds (Nilsson et al. 2008, Chapman et al. 2011), however, it may not always be the smallest individuals that leave as seen in some species (Rikardsen et al. 2004, Alonso et al. 2009). In e.g. salmonids individuals migrate as they become resource limited within the river and therefore seek out better feeding opportunities in the sea or lakes (Rikardsen et al. 2004, Jonsson and Jonsson 2011). A more general view of this hypothesis would be that the individuals that migrates (smallest or largest) would be governed by the habitat in which the individual occupies; where the largest individuals should leave first if they cannot monopolize resources as they will suffer harder when resources are limited (Závorka et al. 2015). Hence, independently if the smallest or largest individuals stay they will choose the strategy which maximizes their reproductive success and life-time fitness (Northcote 1978, Gross et al. 1988, Jonsson and Jonsson 1993). Secondly, the arrival time hypothesis suggests that the competing individual should arrive as early as possible in order to get the competitive advantage for recourses (Lundberg and Alatalo 1992). Individuals that arrive early indicate good phenotypic quality as they can take the cost of early arrival (Lundberg and Alatalo 1992), and occupy the highest quality habitats which may lead to increased reproductive success (Aebischer et al. 1996). Early arrival also increases competitive advantage (prior residency), allowing individual to occupy a profitable territory or habitat (Huntingford and de Leaniz 1997, O'Connor et al. 2000, Jonsson and Jonsson 2011), which may lead to a higher reproductive success as they get access to the "best" habitats. Lastly, the dominance hypothesis which states that large, dominant individuals should be resident when resources are scarce as they are better competitors, forcing subordinates to migrate (Chapman et al. 2011). One could argue that this hypothesis is very similar to the body size hypothesis; however dominance is not always controlled by size (Ward et al. 2004). This hypothesis implies that it would be possible to predict which individuals that migrate by scoring the individuals dominance rank within the population.

One commonly studied form of partial migration is the anadromous migration of salmonids (Jonsson and Jonsson 1993) that refers to a migration that take place between fresh and saltwater. All salmonids have a life-history that starts in freshwater and in most cases a downstream migration is undertaken at some stage in their life-cycle. This migration can be anadromous, or solely within freshwater (Jonsson and Jonsson 2011). The underlying mechanism/decision that determines if the salmonid will migrate or become resident is believed to be taken a year prior to migration (Thorpe et al. 1998, Rikardsen et al. 2004). This decision is primarily based on the growth trajectory of the parr in the summer prior to migration (Fig. 2, Økland et al. 1993, Bohlin et al. 1996, Thorpe et al. 1998, Rikardsen et al. 2004). If a certain genetically determined threshold for migration (M) is reached (Fig. 2) the parr will prepare for migration the following year. The individuals that reach this threshold will maintain apatite and continue to grow, whereas those that fail to reach the threshold will halter their appetite and growth. This will result in two life-history patterns: migratory and residency. To complicate the matter a bit more, there is another threshold; a reproductive threshold, that is assessed prior to spawning in the autumn. Here individuals of both life-history patterns make a new assessment of their lipid content trajectory, and if they are above this threshold they will start investing in reproductive tissue. It is hypothesised that the maturation threshold dominate over the migration threshold, hence an individual that previously decided to migrate can halter this decision and start investing in reproductive tissue (Thorpe et al. 1998). Individuals that fail to reach the maturation threshold remain immature and the fastest growers continue on their migration pathway. This indicates that the body size hypothesis hold for salmonid downstream migration, thou in that sense that the largest individuals are the ones that migrate. However, several studies have failed to show any effect of actual size on migratory tendency but instead suggest that growth potential is the governing factor (Økland et al. 1993, Bohlin et al. 1996). The growth trajectory for a smaller parr could push the individual over the inherited threshold, switching on the preparation for migration (Fig. 2, green line). A larger parr on the other hand can have a lower growth trajectory which puts it under the inherited threshold at the end of the assessment window, hence switching off the preparation for migration (Fig. 2, red line). Hence, the initial size (length) of the parr would be a poor indicator of migration propensity (Økland et al. 1993, Bohlin et al. 1996).

Once the decision for migration is taken the salmonid must adapt for a life in the sea. This transformation is called smolting (smoltification) and includes both physiological and morphological changes (McCormick et al. 1987, Björnsson et al. 2011). This transformation is induced by photoperiod and temperature which stimulates inhibition of prolactin, a hormone that normally inhibits the expression of several hormones. These hormones now instead stimulate the physiological and morphological changes (Björnsson et al. 2011), e.g. the development of chloride cells used for ion regulation in saline environments, silvering of the body, and behavioural changes (Winans and Nishioka 1987, Fyhn et al. 1991, McCormick et al. 1998, Björnsson et al. 2011). When these changes have occurred the smolt can start its descent downstream.

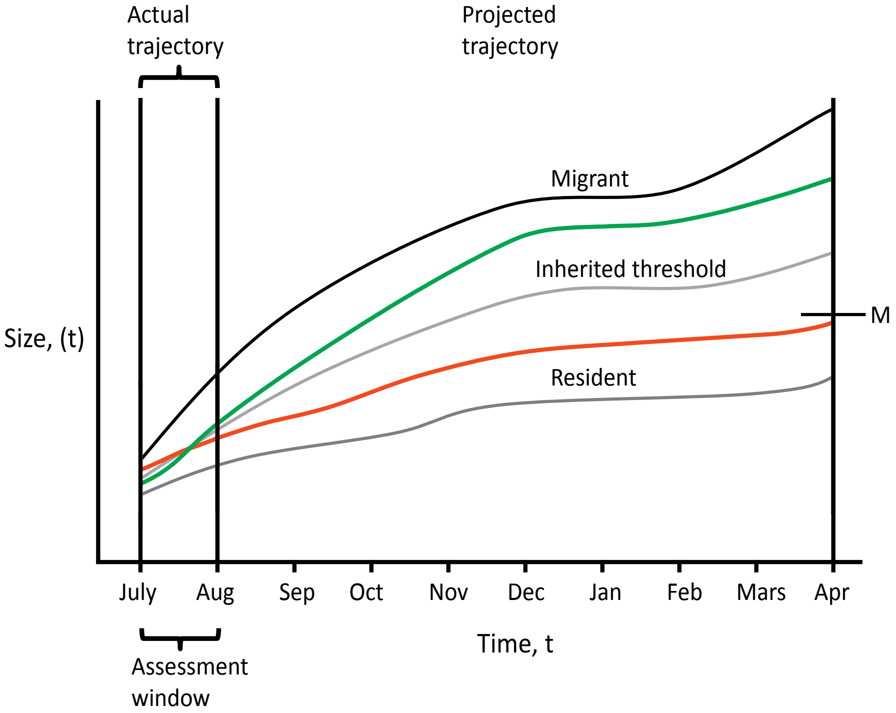

Figure 2: A schematic illustration of the migration assessment window for juveniles. The size trajectories of a theoretical resident (solid grey) and a migratory individual (solid black) are shown relative to an inherited migration threshold (dashed grey), and the absolute migration threshold is marked by (M). The red line show the hypothetical growth trajectory of an initially larger parr that remains resident, and the green line show the trajectory for a smaller parr that develops into a migrant. The figure is modified from Thorpe et al. (1998) and Rikardsen et al. (2004).

Downstream migration of salmonids

Smolt migration occurs foremost during the spring but has been recorded throughout the year (Jonsson and Jonsson 2009) and is believed to be influenced by a range of environmental cues; photoperiod is believed to be the most important, as it is involved in the smolting process, however most likely it lacks importance for the triggering of migration per se (Aldvén et al. 2015a). Other factors, especially temperature and discharge (Fig. 3), have been reported to directly influence the timing of migration (Fried et al. 1978, Grau et al. 1982, Jonsson and Ruud-Hansen 1985, Jonsson 1991, Hvidsten et al. 1995, Hembre et al. 2001, Aarestrup et al. 2002, Aldvén et al. 2015a). Which factors that trigger downstream migration varies between rivers; in some river discharge is the governing factor whereas temperature or both are more important in others (Aldvén et al. 2015a).

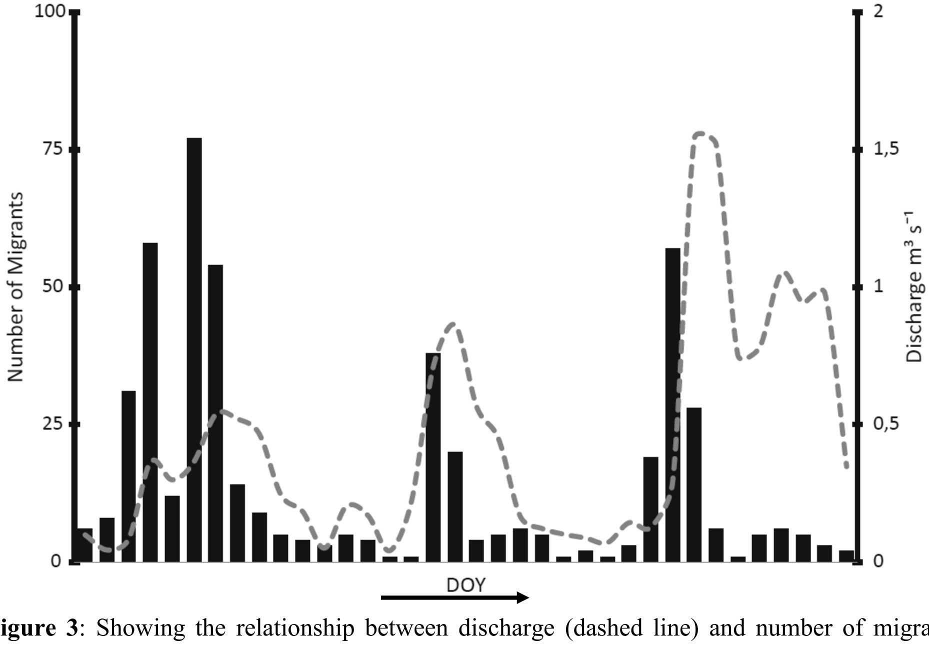

Figure 3: Showing the relationship between discharge (dashed line) and number of migrating smolts (bars) during the spring migration (March to May). The data are pooled and consists of PIT-tag data from Kärraån and Bodeleån from 2012 to 2015. The x-axis is showing increasing day of year (DOY).

To highlight the complexity regarding the triggers of downstream migration I will show an example from four rivers along the west coast of Sweden (Fig. 4). Here, I also investigate the potential effect of climate change on the timing of outward migration. The driving factors for migration was investigated by pooling migration data from smolt traps from 1965 to 2012 in four rivers on the Swedish west coast (Anråse å, Himleån, Norrån, and Slereboån). Air temperature, discharge, year and river, were examined for normality, collinearity, heterogeneity of variance and outliers using the protocol given in Zuur *et al.* (2010). To avoid getting biased results from the discharge due to differences in stream sizes, the discharge data was standardized by dividing the measured discharge with the size of the drainage area creating a discharge index (m^3 / s / km^2) as described in Searcy (1959), here after referred to only as discharge. Collinearity was not detected among factors, and all factors were included in the model. Zero inflation in the response variables (number of sea trout smolts) indicated a negative binominal distribution, and due to this non normality generalized additive models (GAMs) were used to model the response variable against temperature and discharge, using river as an interaction term and sampling year as a covariate (Eq. 1). The analysis was carried out using the package mgcv in R (Team 2008, Wood 2011).

$$Y = \alpha + \beta + f(\delta){:}\gamma + f(\theta){:}\gamma + \tau + \varepsilon \qquad \text{(Eq. 1)}$$

where Y is the number of smolts, α is the intercept, β is the slope, δ is the discharge, θ the air temperature, γ the river of sampling, τ the year of sampling and ε the estimated error of the model. A stepwise reduction in non-significant factors in the model was used giving a final model where year was removed (Eq. 2):

$$Y = \alpha + \beta + f(\delta){:}\gamma + f(\theta){:}\gamma + \varepsilon \qquad \text{(Eq. 2)}$$

The model was validated by testing for homogeneity and independence. The GAM model for downstream migration showed that both discharge and temperature significantly affect downstream migration timing (GAM: adj. R-sq. = 0.638, deviance explained = 25.1%, n=889), however in some streams only one of the factors affected downstream migration (Table 1).

Table 1: Generalized additive models showing relationship between number of migrating smolts, river discharge and air temperature from four rivers on the west coast of Sweden. Year was excluded in the final model. The estimated degrees of freedom (edf) for the smoother and the reference degrees of freedom (Ref. df) were used by the model to calculate F-statistics are also presented.

Full model

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	2.8129	0.1497	18.79	<0.001
Year	0.03034	0.03368	0.901	0.368

Smooth terms	edf	Ref. df	F	p-value
Discharge: Anråse å	4.682	5.063	5.274	**<0.001**
Discharge: Himleån	2.278	2.852	5.144	**0.00208**
Discharge: Norrån	8.202	8.822	6.686	**<0.001**
Discharge: Slereboån	4.778	5.592	1.213	0.2969
Temperature: Anråse å	1.401	1.701	0.758	0.4351
Temperature: Himleån	4.574	5.487	2.921	**0.01041**
Temperature: Norrån	5.906	6.807	6.462	**<0.001**
Temperature: Slereboån	3.357	4.129	2.579	**0.03466**

In the rivers Anråse å, Himleån, and Norrån increased discharge was found to positively affect the downstream migration when above 0.02 m^3 / s / km^2, whereas no such effect was found in Slereboån (Fig. 5). At discharges higher than app. 0.03 m^3 / s / km^2 the effect of discharge was found to be varying between rivers and the effect on number of migrants could be either positive or negative. The importance of temperature was generally weaker compared to discharge but was found to stimulate migration in three of the rivers (Himleån, Norrån, and Slereboån; Fig. 6) but to a variable extent; in Himlån and Slereboån. A positive effect was found for temperatures above 10 ºC until the temperature reached 15 ºC where the effect could go in any direction. In Norrån a positive effect of temperature was found for temperatures between 7 and 10 ºC after which a negative effect was found. That the triggers and timing of downstream migration differs in different locations is probably due to local genetic adaptations (Antonsson and Gudjonsson 2002), or a response to spatial and temporal environmental variations (Jonsson and Ruud-Hansen 1985, Hembre et al. 2001). Due to this complexity it is not surprising that previous studies have shown that downstream migration of smolts starts at different times, both between adjacent rivers but also within rivers between years (Hvidsten et al. 1995, Davidsen et al. 2005, Stewart et al. 2006).

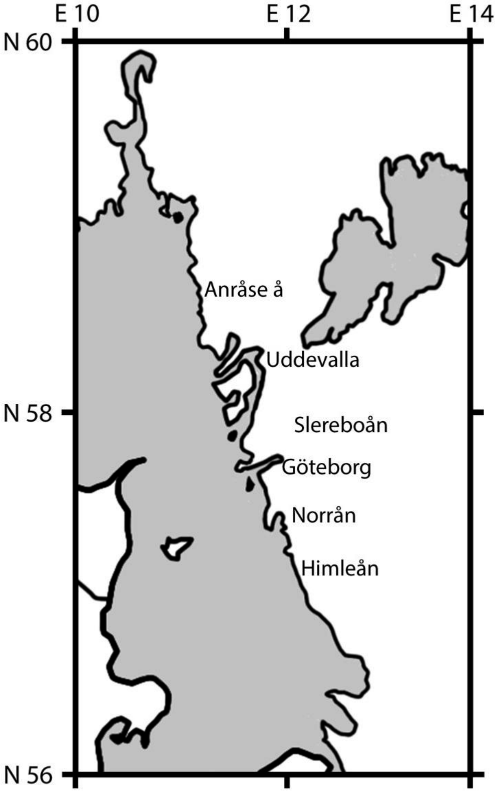

Figure 4: A map showing the Swedish west coast and the approximate position of the rivers used in the models.

The downstream migration of smolts is often associated with poor survival (Jepsen et al. 1998, Olsson et al. 2001), often as a consequence of anthropogenic changes altering and obscuring migratory routes, e.g. weirs, dams and wetlands (Poff et al. 1997, Olsson et al. 2001).

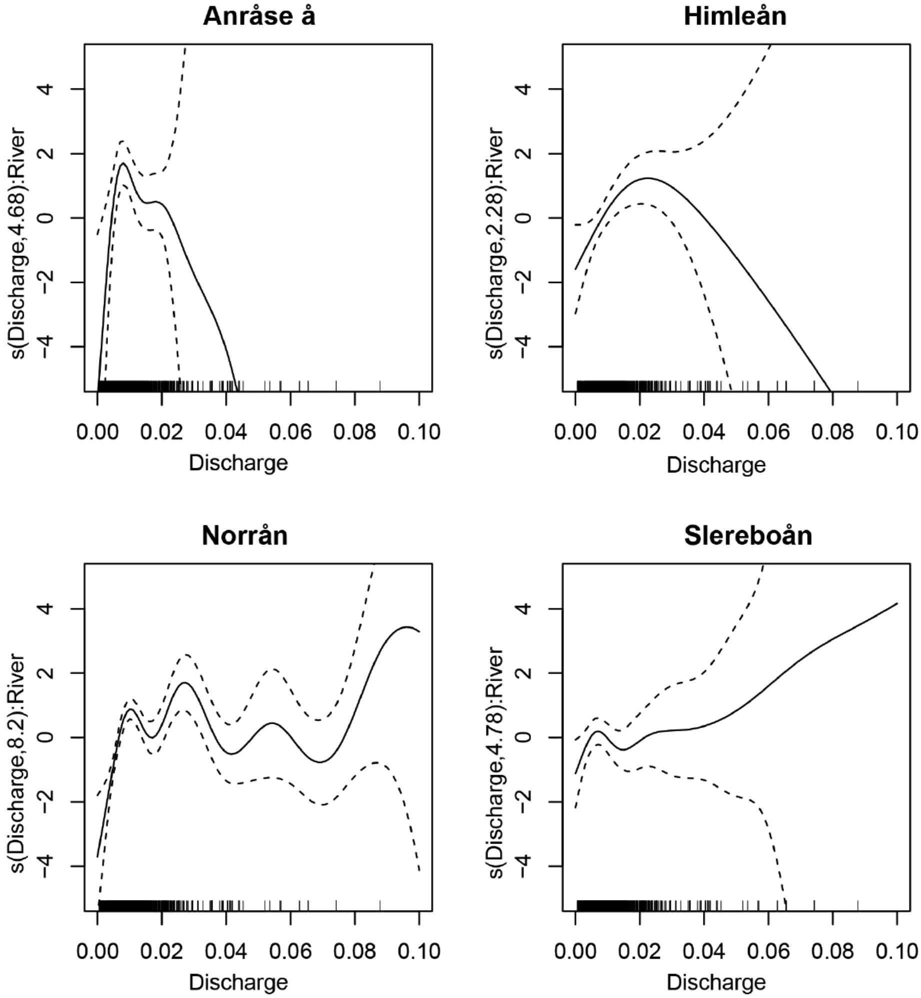

Figure 5: Showing the GAM smoothers (solid line) with 95%-confidence bands (dashed lines) for the interaction between discharge and river for different flow regimes, in the four different rivers. Where the y-axis shows the deviation from the mean (zero). The lines on the x-axis indicates individual cases, i.e. an observation of number of migrants for a certain level of discharge.

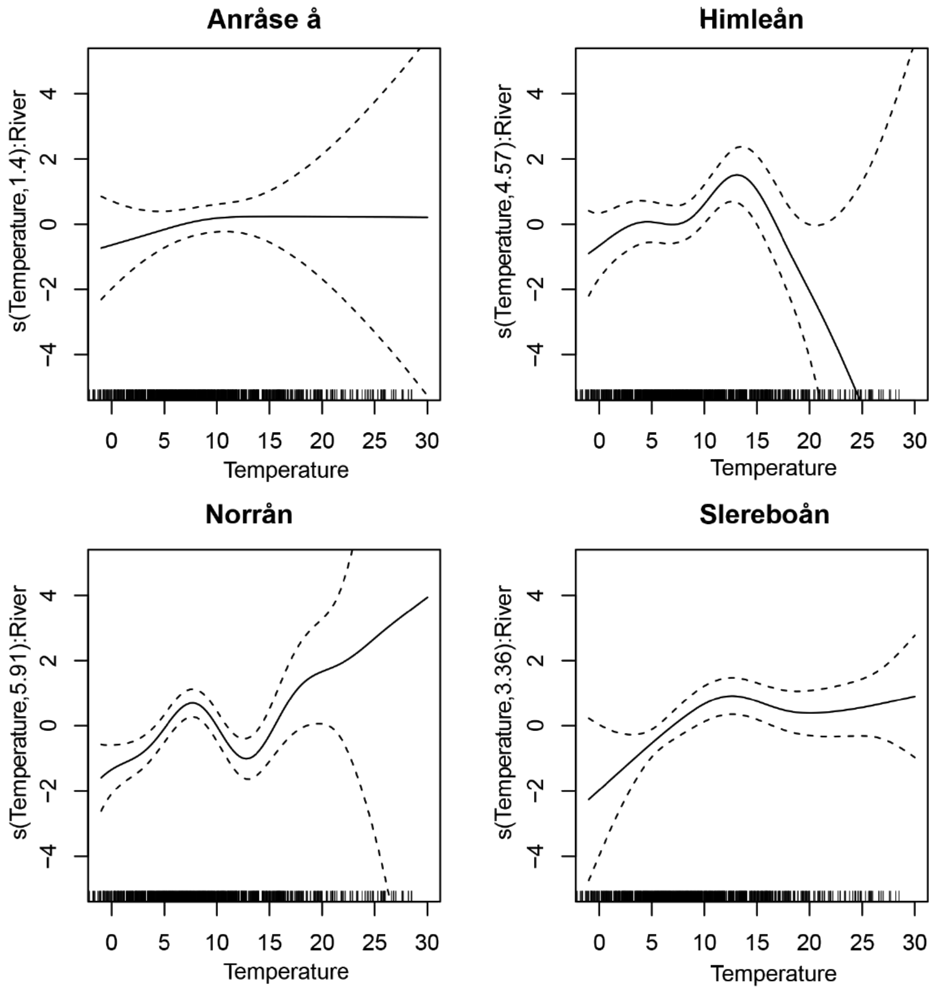

Figure 6: Showing the GAM smoothers (solid line) with 95%-confidence bands (dashed lines) for the interaction between air temperature and river for different air temperatures, in the four different rivers. Where the y-axis shows the deviation from the mean (zero). The lines on the x-axis indicates individual observations, i.e. an observation of number of migrants for a certain air temperature.

The artificial pools that are created behind these man made obstacles often become a habitat for predators such as pike (*Esox Lucius*), zander (*Sander lucioperca*) and cormorant (*Phalacrocoracidae*), hence increasing predation pressure on smolts (Jepsen et al. 1998, 2005, Koed et al. 2006). As a consequence of this predation pressure, downstream migration is repeatedly observed to be primarily nocturnal early in the migratory season then shifting to diel during later spring migration (Thorpe et al. 1994, Ibbotson et al. 2006, Aldvén et al. 2015a). This pattern is believed to be a predator avoidance response, where theory states that the escape response of the smolts increases with temperature which enables them to take the risk of migration during the day when the potential predation risk is higher (Rikardsen et al. 2006, Hvidsten et al. 2009). Another observed anti-predator response found during smolt runs is shoaling (Hvidsten et al. 1995, Davidsen et al. 2005, Stewart et al. 2006). These shoals can be single species as well as multi species, i.e. Atlantic salmon (*Salmo salar*), brown trout (*Salmo trutta*) and roach (*Rutilus rutilus*) together or in different configuration (Jonsson and Jonsson 2009, Aldvén et al. 2015a).

Sea trout post-smolt migration

Smolts are termed post-smolts once they have entered sea water during their downstream migration. Sea entry and the initial migration in estuaries have been observed to be foremost nocturnal (Moore and Potter 1994, Moore et al. 1998, Koed et al. 2006, Thorstad et al. 2007, Aarestrup et al. 2014, Aldvén et al. 2015b), however this movement has on occations been reported to take place during the day (Moore et al. 1998, Aarestrup et al. 2014). This movement has been found to follow tidal cycles with post-smolts moving through estuaries at ebbing tides, or the period of slack water between two high waters (Moore and Potter 1994, Thorstad et al. 2007). The transition between fresh and salt water is often associated with high mortalities for post-smolts, ranging from 12-49% (Koed et al. 2006, del Villar-Guerra et al. 2014, Aldvén et al. 2015b). Post-smolt migrations through estuaries are suggesting active and directed swimming (Thorstad et al. 2007) or similar to that of passively drifting objects (Moore and Potter 1994). Post-smolts utilize the top layer of the water column (0.6-7 m) independent of the depth at the locality (Lyse et al. 1998, Ruud 2015) and tend to stay close to their natal rivers at initial sea entry. However, later on they display a variety of dispersal behaviours, with some moving large distances while others remain close to natal rivers (Finstad et al. 2005b, Thorstad et al. 2007, Middlemas et al. 2009, Manel-la et al. 2011, Davidsen et al. 2014, del Villar-Guerra et al. 2014).

As the post-smolt progresses further out from the estuaries and fjords the nocturnal movement pattern breaks down and a diel migration pattern occurs (Thorstad et al. 2007, Aldvén et al. 2015b). Within fjords, post-smolts have been found to stay close to the shoreline in the fastest moving section of the water column (Lyse et al. 1998, Thorstad et al. 2007). del Villar-Guerra et al. (2014) also found a tendency for post-smolts to avoid areas with narrow channels and tidal flats along the embankments. Migration speeds within fjord systems often vary between and within study sites, with a range from 0.003 to 0.56 Body lengths per second (Thorstad et al. 2004, 2007, Finstad et al. 2005b, Aarestrup et al. 2014). Finstad (2005) recorded a gradual increase in migration speed of trout as they moved out towards the sea, whereas Aarestrup et al. (2014) and Aldvén (**Paper IV**) found a gradual decrease in migration speeds when the post-smolts progressed towards the sea. This could be reflected in the different migration strategies that have been observed; e.g. in Sweden and Denmark two different migration strategies have been observed; fjord residence or sea migratory (del Villar-Guerra et al. 2014), whereas fjord residency seems to be the case for populations at higher latitudes (Finstad et al. 2005b, Rikardsen et al. 2007b). In Denmark as many as 53 % of the post-smolts left the fjord area whereas only 17 % left the fjord system in Sweden (del Villar-Guerra et al. 2014; **Paper IV**). Migration towards the sea are associated with mortalities between 21-65% (Thorstad et al. 2007, Aarestrup et al. 2014, Aldvén et al. 2015b), or between 0.63 to 2.08 % per km (Aarestrup et al. 2014, Aldvén et al. 2015b).

The time spent in the sea varies a lot between populations and latitudes. Studies from Norway showed that the time at sea of first time migrants varied from 68 ± 21days in northern Norway to 6-9 months in the middle of Norway (Berg and Berg

1987, Jonsson and Jonsson 2009, Davidsen et al. 2014). Further, Jonsson and Jonsson (2011) claim that the period spent in the sea varies from 1 month to 5 year, without specifying any geographical differences. Total mortality rates for the time at sea for post-smolt can also vary a lot between populations. In Norway this numbers vary from ca 1-26.6% depending on when they migrate to sea (Jonsson and Jonsson 2009, Davidsen et al. 2014, Jensen et al. 2015). In Burrishoole Ireland, the sea survival during 1975-1994 varied between 1.8-66% for sea trout smolts (Poole et al. 1996). In the Norwegian systems this survival was proposed to be affected by a mismatch in sea arrival and food abundance in the sea, where a lower survival was observed for fall migrants that arrive in the sea when prey items were scarce (Jonsson and Jonsson 2009). In the Irish system the large variation in sea survival was caused by the establishment of salmon farms which increased the abundances of sea lice (*Lepeophtheirus salmonis*) casing mortality rates to increase substantially.

Upstream migration of spawners

The timing of the spawning migration back to the river may vary between populations of salmonids but also within a population (Fleming 1996, Klemetsen et al. 2003). It seems likely that the maturation at sea is govern by growth rate at sea or size, as it has been shown that a high growth rate at the first year at sea yields a later return and maturation in Atlantic salmon *Salmo salar* (Jonsson and Jonsson 2007), hence a low growth rate at sea during the first year yields an earlier return. In aquaculture it has been proposed that an interaction between genotype and environment plays a role, and that the age of maturity might be a heritable trait (Gjerde 1984, Wild et al. 1994). Recent studies on *S. salar* also confirm that maturation at sea is genetically controlled (Ayllon et al. 2015, Barson et al. 2015). The variation in time spent in the sea is large and some individuals stay in the sea for a couple of months before spawning whereas others stay several years in the sea before returning (Jonsson and Jonsson 2011). However, the initiating factors (triggers) for homeward migration are not yet known (Hansen and Quinn 1998). The return migration is believed to be split into two parts; first the orientation to the coastline from the feeding area, followed by the second part of the migration which is a precise orientation from coastal waters to the native river (Hansen et al. 1993). The mechanism behind the orientation from the feeding ground to coastal waters remains a mystery; some suggests that a compass is used for this orientation, e.g. magneto reception, polarized light, or celestial objects (Jonsson and Jonsson 2011). The precision of homing varies between populations and species; e.g. *S. salar* can show very precis homing (97-99 %), whereas *S. trutta* generally show lower fidelity (ca 85%) to their home river (Berg and Berg 1987, Fleming 1996, Ísaksson et al. 1997, Degerman et al. 2012). It is believed that the smolt imprint the scent of their native river during downstream migration, hence learning how their home river smell, allowing them to find the river once it is time to return for spawning (Lucas et al. 2001). The smell of the river has been proposed to consist of free amino acid compositions as seen in Pacific salmon *Oncorhynchus sp.* (Ueda 2012, 2014). Once they reach their home river they do not necessarily enter the river directly. In some systems the spawners wait for favourable environmental conditions before migrating upstream. However, the parameters that triggers upstream migration might differ between streams; in some streams a slower water flow seems to be favourable for upstream migrations (Jonsson et al. 1990, Trepanier et al. 1996), whereas the smaller streams on the west coast of Sweden displays an increased upstream movement during peak flows (Berntsson and Johansson 1977). Also the distance from the mouth of the river to the spawning ground plays an important role in the timing of upstream migration (Thorstad et al. 2001, Finstad et al. 2005a). If the distance is large the migration starts earlier compared to if the migration is short, and in the extreme cases migration may start one year before the spawning as seen in the Loire, France (Jonsson and Jonsson 2011).

In the river, the migration can be divided into four phases (Økland et al. 2001); first there is an upstream movement from the estuary, a phase that can vary from a few days to a couple of months depending on the distance to the spawning ground and how many obstacles (e.g. waterfalls and dams) that needs to be bypassed (Thorstad et al. 2007). The second phase is a search phase, here the fish moves up- and downstream to the position in which it later spawns (Økland et al. 2001). This search phase is believed to be important for the fish to find a suitable spawning ground and in the case for *S. salar* to find the exact tributary where they hatched (Fleming 1996). The search is also important to find a good place for the third phase; the holding phase. During the holding phase the spawner hold its position until the final phase; the spawning phase.

Post spawning migration of sea trout

After spawning, the individuals that survive (kelts) may once again enter the sea to feed before the next spawning. The outward migration of kelts can take place directly after the spawning or 1-6 months later (Bendall et al. 2005, Östergren and Rivinoja 2008, Kraabøl et al. 2008). In larger rivers the outward migration of kelts often takes place during the following spring and early summer (Berg and Berg 1989, Klemetsen et al. 2003, Östergren and Rivinoja 2008, Aldvén et al. 2015b), whereas they seem to leave directly after spawning in smaller river (Aldvén unpublished data). As seen in smolts the transition between fresh and salt water occurs during the night (Bendall et al. 2005, Aldvén et al. 2015b). Residence time within estuaries has been found to be short, often with a slow progression rate (Bendall et al. 2005, Aldvén et al. 2015b). This progression rate becomes slower the further away from the river they migrate (Aldvén et al. 2015b, Aarestrup et al. 2015). At sea, veteran sea trout spend >90% of their time in the upper 3 m of the water column, and occasionally undertake deeper dives (Rikardsen et al. 2007b). They are often found in the littoral zone and to a lesser extent in pelagic areas (Jensen et al. 2014, Eldøy et al. 2015). During the marine feeding migration, the veteran migrants are opportunistic feeders but with an increasing use of marine prey fish by larger sea trout (Rikardsen et al. 2007a). Similar to post-smolts, the duration of stay within the sea varies between latitudes and they stay within the sea varies from 1 to 366 days (Berg and Berg 1989, Klemetsen et al. 2003, Rikardsen et al. 2007a, Jonsson and Jonsson 2009, Jensen and Rikardsen 2012, Aarestrup et al. 2015). The time spent at sea have been found to be positively correlated to both body length and smolt age, but negatively correlated to the time of sea entry (Eldøy et al. 2015). However, at northern latitudes the sea sojourn can also be prolonged by high sea temperatures during long summers (Berg and Berg 1989). Veteran migrants also display a large variety of migration patterns within the sea in terms of migration distance; Eldøy et al. (2015) found that they spent 68% of time during their marine residence within 4 km from the river mouth and individual with poorer body condition prior to migration migrated longer distances, used pelagic areas more often and had an earlier return to freshwater compared to short distance migrants. However, migration distance can vary between populations and in the Baltic the migration distance for sea trout can be a couple of km from the native river to sea trout migrating from the southern most part to the Bothnian bay, a distance of over a thousand kilometres, and even into the North Sea (Svärdson and Anheden 1963, Kallio-Nyberg et al. 2002, Bartel et al. 2010, Degerman et al. 2012). Long distance migrants have also been reported from Scotland and Sweden, where fish from both sites have been recaptured of the Norwegian west coast, and in the former case at the inlet to the Baltic Sea (Berntsson and Johansson 1977, Pratten and Shearer 1983). Marine survival for veteran migrants is often between 18-50% (Berg and Jonsson 1990, Bendall et al. 2005, Aarestrup et al. 2015), hence larger than for smolts.

Aim of this thesis

The overall aim of this this thesis was to investigate migration patterns in smolts and kelts of sea trout during their downstream migration and initial movement at sea. More specifically, I aimed to:

a) Investigate which environmental cues that trigger smolt migration (**Paper I** and **IV**)

b) Study how the sea trout stock has developed over time as well as predict what possible effects future climate change might have on sea trout stocks (**Paper II**).

c) Study how many genetic stocks of sea trout there are on the west coast of Sweden and how much these potential stocks overlap (spatially) in their distribution within the sea (**Paper V**).

d) Investigate movements of smolts and kelts from the river and within the sea, and to identify different migration strategies within and between rivers (**Paper III and IV**)

e) Use the results to suggest improvement and increase the efficiency of future stock management in the region.

It would, however, be presumptuous to claim that the summarized data from these studies alone would be enough for a good management. Therefore the conclusion of this thesis will also include suggestions for the focus of future studies.

Notes on methods

The studies in this thesis are based on both data collected from monitoring as well as experimental studies in the field. The following section will give a detailed overview of methods used in this thesis.

Field data

In **Paper I** we wanted to evaluate a smolt production model (developed by Nilsson et al. 2010) by comparing trap data with modelled data, as well as investigate which environmental cues that trigger downstream migration. The system used was Himleån (Varberg), a 38 km long river that drains into an open coastal system. A smolt-trap was operated during two consecutive migration periods in 2011 and 2012 (see **Paper I** for a figure and details about the trap). The river had an average spring discharge of 2.25 $m^3 s^{-1}$ (range 0.72-7.13 $m^3 s^{-1}$) over the two years the trap was operated. The model used for smolt production estimates included data on juvenile abundances; available habitat, winter survival, and migration mortality (see **Paper I** for details). The assessment of which environmental cue that trigger downstream migration was evaluated using non-linear models were temperature and discharge were chosen in the final models (due to auto correlation among variables) as they are considered to be the most important for triggering downstream migration. From the catches in the trap a subsample of individuals were equipped with hydro acoustic transmitters, overall 179 smolts and 40 kelts, between 2011 and 2012 (**Paper III**). The tags were surgically inserted into the gut cavity of the trout and closed with two sutures. The hydro acoustic transmitters allowed for tracking of individual trout from the river and out into the sea (Box 1). The aim of this study was to investigate sea trout movements during the initial phase of their anadromous migration. The tracking was performed by setting up several arrays of receiver in the river, estuary, and coastline (Figure 1 in **Paper III**). Differences in migration strategies were then tested against the following range of environmental and morphological traits; body length, stage (smolt or kelt), sex, river temperature and river discharge.

In **Paper IV** we performed a similar experiment where we tagged sea trout smolts from two adjacent rivers (Bodeleån and Kärraån [Uddevalla]), but this time the rivers drain in a fjord system (Byfjorden). The rivers are similar in morphology, size, length, and mean annual discharge (0.247 m^3 s^{-1} in Bodeleån and 0.249 m^3 s^{-1} in Kärraån). The temperature varied between the rivers and Kärraån is on average 2 ºC warmer compared to Bodeleån (Mean±SD: Kärraån; 13.1±4.4, and Bodeleån; 11.3±3.7 during March to July).

The aim of the study was to evaluate how two different populations of sea trout overlap in their migrations patterns in the sea, and to investigate how growth rate affects smoltification and timing of migration. In 2013, 80 smolts were caught by electrofishing as pre-smolts and double tagged with hydro acoustic transmitters and PIT-tags (Passive integrated transponder). The reason for this was that both rivers were equipped with PIT-tag antennas allowing us to monitor a potential back migration long after the battery in the hydro acoustic tag was depleted. The tracking within the sea was similar to Himleån using hydrophones, and the fjord was closed off by several gate ways of receivers (see Fig. 1 in **Paper IV**). In addition, scale samples were taken for back calculation of growth rate during the first and second year (Závorka et al. 2014).

Collected data from monitoring

In **Paper II** we used available electrofishing data from the Swedish electro fishing register (SERS) to evaluate population abundances of brown trout parr on the west coast of Sweden between 1985 and 2014. In total 134 electrofishing sites in 104 streams, along the entire 320 km long west coast was included in the analysis, covering 4887 electrofishing occasions. From the data, population abundances were calculated according to Bohlin et al. (1989). If no successive removal was performed, abundances were estimated based on one occasion using data on catch

Box 1: Hydro acoustics explained

A hydro acoustic tag is a transmitter that transmits a specific individual coded signal to a receiver (hydrophone), located up to kilometre away from the tag. The signal is a sound signal that creates a pressure wave spread omni-directional through the water. The frequency of the tags (69-180 kHz) does not allow the signal to propagate through air more than a couple of cm, therefore the receiver needs to be submerged in order to record the signal and position the fish (Fig. A).

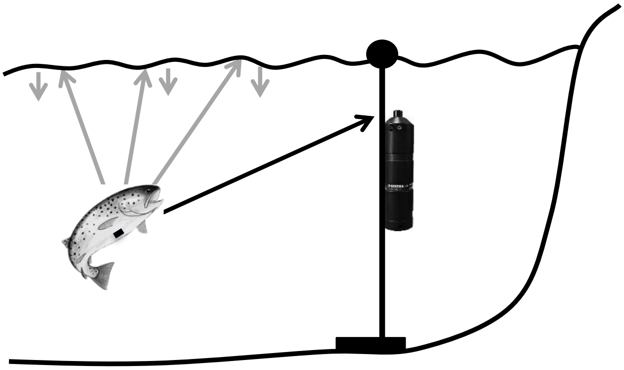

Fig. A: A schematic of how the hydro acoustic setup works and how the signal propagates through water.

The transmitted signal can be used to identify individual fish, either by a unique combination of frequency and pulse rate (time between transmissions) or by using coded signals (Fig. B). The coded signals consist of a unique sequence of pulses in time that is recognised by the receiver but not hearable for the human ear.

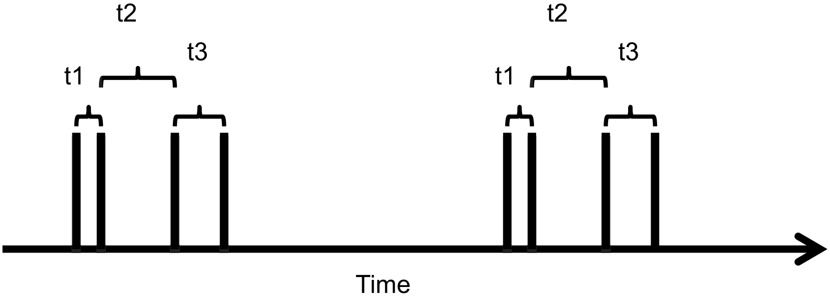

Fig. B: The figure shows a schematic example of a hydro acoustic signal. The signal consists of four sound pulses, and the code consists of three time intervals, i.e. from the start of each sound pulse to the next (t1, t2 and t3). The receiver can automatically recognise and identify this code.

probabilities from SERS. Mean densities of parr (individuals per 100 m^2) of brown trout (0+ and 1yr and older) for each year was calculated using an ANCOVA. Standardized densities across the west coast of Sweden were incorporated in the model by including size of the water course, date of sampling, altitude of the sampling site, depth of the locality (0+ only), and the proportion of lakes in the system. By coupling this data with the mean annual air temperature on the west coast we could examine the effects of regional climate change on parr abundances and sizes. Lastly we gathered data of smolt sizes (fork length) from old reports (grey literature) and scientific papers from the west coast of Sweden to examine the effects of temperature on smolt sizes over the last 50 years.

Genetics

In the fifth study (**Paper V**) we used genetics to investigate migration patterns and population structure along the coast. For this purpose, tissues were sampled from adult fish returning to spawn in 20 streams along the west coast. This base line were then compared with angler caught sea trout in the sea, allowing us to assign fish caught on sport fishing to a likely stream or region from origin. Sampling in the stream also gave us data on straying, as a low straying rate would mean many genetically different populations whereas high straying would mean few. The main aim was to investigate genetic differentiation of sea trout on the west coast of Sweden, as well as evaluating the usefulness of this method when it comes to studying migration patterns of sea trout in the sea. Genetic variation was analysed using 3852 Single Nucleotide Polymorphism (SNP) marker.

Main findings and discussion

This section will summarize the papers included in the thesis as well as shortly discuss the main findings:

Environmental cues and downstream migration (Paper I)

In **Paper I** we investigated the effect of environmental cues on downstream migration as well as testing the reliability of an improved smolt production model in Himleån on the west coast of Sweden.

We found that both discharge and temperature affected the initiation of downstream migration, however the effect was found to vary between years; in 2011 the downstream migration was triggered by temperature whereas it was triggered by discharge in 2012. The diverging effects can be explained by the absence of rain in 2011 forcing the smolts to migrate downstream during low discharge when the temperature in the river increased. It has been shown that desmoltification rates increases when the temperatures reaches 10ºC (Jonsson and Jonsson 2011), hence forcing the smolts to either take the risk of migration or remain and wait another year before migration. We also found that the smolts predominantly migrated during night in the beginning of the season but shifted to a diurnal migration pattern later in the season. This is believed to be an anti-predator response where the fish's reactivity responses increase with the temperature allowing the smolts to migrate during the day (Thorpe et al. 1994). At the same time we also did the novel observation that the smolts formed inter species shoals consisting of *S. trutta*, *S. salar* and *R. rutilus*, which probably is another anti-predator response (Aldvén et al. 2015a).

The smolt production model gave an overestimation of smolt numbers of 18% and 19% for 2011 and 2012 respectively. This overestimation could be a consequence of several factors; the fixed estimate of 30% of the parr becoming smolts, the selection of electrofishing sites or due to an underestimation in the smolt trap. The last factor can have a large effect as we needed to open the trap during very high flows. These results suggest that it is possible to improve the model further e.g. by improving the habitat mapping, by having a more accurate estimate of mortality during migration, and by getting better estimates on the parr to smolt percentage.

Environmental effects on parr and smolt sizes (Paper II)

In **Paper II** we investigated the effects of climate change on parr and smolt growth and abundances. Data from the last 30 years was used in order to assess the climatic impact on brown trout populations on the west coast of Sweden.

The results showed that recruitment (0+ densities) had remain stable over the last 30 years, although the between year variation was large (Fig. 1 in **Paper II**). At the same time the abundance of older cohorts (1yr and older) showed a significant decrease (Fig. 1) whereas the mean size of the largest 0+ had significantly increased (Fig. 2 in **Paper II**). This increase was found to be significantly correlated with the mean annual air temperature (Table 1 in **Paper II**). Smolt size was also found to be affected by an increased air temperature and showed a significant negative correlation with temperature over time (Fig. 3 & 4 in **Paper II**).

We suggest that the increase of 0+ parr size may be a result of a prolonged growth period due to milder climate as suggested by Jonsson *et al.* (2005), or as a consequence of a better feeding regime at the time for first feeding. This is supported by the significant effect of increasing temperature during late winter and early spring on 0+ parr size (Table 1 in **Paper II**). The decreased numbers of older cohorts could not be explained by lower recruitment or increased mortality, as anecdotal reports instead suggests an increased number of fish within the sea. Another explanation could be that some 0+ do not grow during the first year but remain at a size of 35-50 mm (fork length), which indicates high competition within cohorts (Nordwall et al. 2001). Increased competition could instead lead to an increased number of smolt that migrates as 1yr, which has been observed in *S.*

salar (Jonsson et al. 2005). A large migration of 1yr smolts would lead to decreased competition from older cohorts on 0+ parr, which enables 0+ parr to exploit habitats normally occupied by older cohorts (Kaspersson et al. 2012), which in turn allows 0+ parr to become larger. This argument is also supported by the decreased smolt size over time. The ecological consequences of this alteration in life history are hard to predict. It is however, possible that the reduction in smolt size could affect population numbers in the long run, as increasing sea temperatures yield better growth rates and early maturation (Scarnecchia 1983). This could potentially lead to an increase in one-sea-winter and zero-winter (return migration the same year as smolt migration) spawners. As smaller individuals have lower fecundity compared to multi-sea-winter sea trout (Jonsson et al. 1996, Jonsson and Jonsson 2004), this could lead to lower recruitment and hence a lower smolt production. On the other hand increased river temperature leads to increased river productivity, which could contradict a potential lowered production (Hannesdóttir et al. 2013). Another explanation could be that the rivers on the west coast of Sweden have a stock recruitment relationship similar to the Beverton-Holt type of model (Fig. 7). This model has been observed in several systems for Atlantic salmon (Chadwick 1985, Poole et al. 1996), whereas the more dome-shaped Ricker stock recruitment relationship (Fig. 7) has been found in others (Crozier and Kennedy 1995, Dumas 2003). The Ricker model yields a decline in recruitment when the spawning biomass has passed a maximum yield threshold. The Beverton-Holt relationship, on the other hand, states that as the number of eggs that is deposit increase there is first a rapid increase in the population which soon levels out and remain more stable. The difference between these two models is that the density dependent parameter is in the exponent (β) for the Ricker model (Eq. 3) in contrast to (α) in the Beverton-Holt model (Eq. 4).

$$R = \alpha S e^{-\beta s} \quad \text{(Eq. 3)}$$

$$R = \alpha S/(1 + \beta S) \quad \text{(Eq. 4)}$$

In the equations above, R is the recruitment, α and β are the parameters of the model and S is the population size. As we have not observed any decline in recruitment it is likely that the streams on the west coast of Sweden have reached this "flat" point of the curve (Beverton-Holt, Eq. 4), hence not showing an increase in population numbers. However, as egg deposit increases within cohort competition should increases and only the fastest grower should be able to find and defend a territory. It is therefore possible that parr growth rate have increased over time due to increased competition as a consequence of the increase in temperature and that a continued temperature increase further selects for fast growth rate.

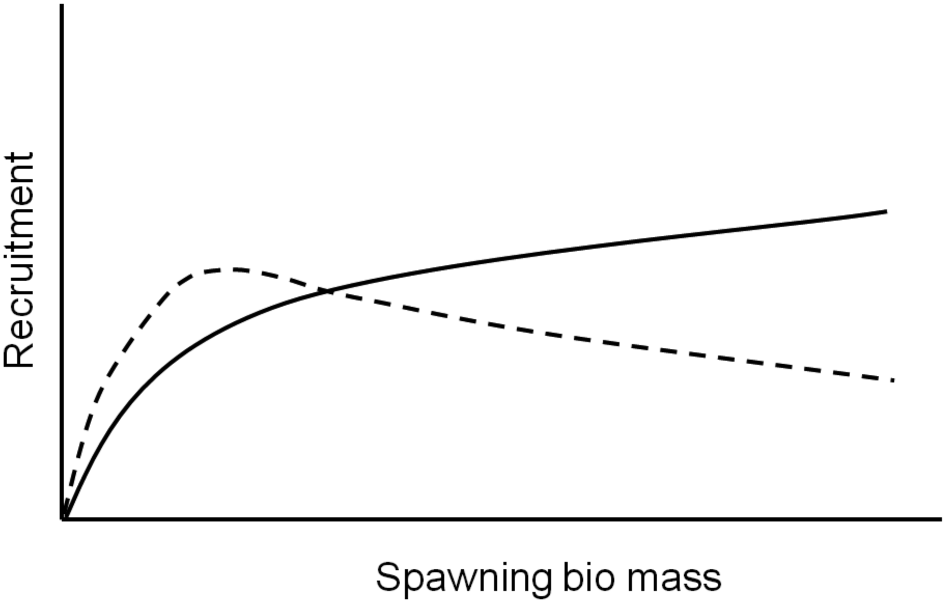

Figure 7: Showing a Beverton-Holt type of stock recruitment relationship (solid line) and the Ricker type stock recruitment relationship (dashed line)

Migration through a complex coastal habitat (Paper III)

In **Paper III** we investigated migration patterns of sea trout kelts and smolts through a complex costal system. The study site was again Himleån and its estuary and the surrounding coastline on the west coast of Sweden (Fig. 1 in **Paper III**).

The migration through the river and estuary was predominately nocturnal, whereas no such trend was found along the coastline (Fig. 3 in **Paper III**). This pattern is likely to reflect a predator response as the river and estuary in this system to a large extent consists of a bird sanctuary (Fig. 1 in **Paper III**). Migration speed decreased as the individuals made their way through the system, and the speeds did not differ between smolts and kelts. The lowered migration speed in the estuary is most likely a consequence of the sea trout searching for a way through this shallow area, whereas the even lower groundspeed along the coast probably is an effect of the sea trout foraging (Jepsen et al. 1998, Thorstad et al. 2004). Most individuals choose to use the northern exits through the estuary (Fig. 4 in **Paper III**). It has been hypothesised that sea trout follow the prevailing currents once the reach the coastline (Suardson et al. 1982, Degerman et al. 2012), and this was found in 2011 but not in 2012. Why this conflicting pattern between the years was observed, remains to be investigated.

Mortality rates between years varied but were greater in 2011 compared to 2012. The difference was probably due to a lower discharge in 2011, hence leading to a greater mortality. A tendency of greater mortality in smolts compared to kelts was found in 2012. This finding goes in line with theory that smaller individuals are more susceptible to predation due to gape limitation (Skov et al. 2011). However, this pattern was not found in 2011 probably due to the overall high mortality of both kelts and smolts as a consequence of the low discharge.

Fjord migration of two populations of sea trout (Paper IV)

The aim of this study was to test if fast growing parr smoltified and migrated out earlier compared to slower growing parr, and to investigate if migration pathways differed between two neighbouring rivers. The study was conducted in the two neighbouring rivers; Bodeleån and Kärraån entering into a fjord (Byfjorden, Uddevalla; Fig. 1 in **Paper IV**). From these two rivers a total of 80 smolts (40 from each river) were equipped with hydro acoustic transmitters.

Migration occurred in two distinct clusters; one early and one late in both rivers but these two groups did not differ in growth rate or size. Migration pathways were similar between the two rivers, however, sea entry was found to be later for smolts in Kärraån and they stayed for a shorter period within the inner fjord compared with fish from Bodelån (Fig. 3 & 4 in **Paper IV**). This delayed sea entry caused these smolts to be delayed in their progression through the fjord system (Fig. 5 in **Paper IV**). This difference could not be explained by environmental factor (e.g. temperature), and is more likely a consequence of differentiation in physiological smoltification between the two populations. This has previous been observed between stationary and migratory brown trout (Nielsen et al. 2003, 2006), but not within migratory group of trout.

The earlier migratory group had a longer residence time in the inner part of the fjord, which is likely to reflect the habitat quality outside the rivers. The characteristics of the area outside the rivers are similar but the available area outside Kärraån is 30% smaller compared to the area outside Bodeleån. These areas have been found to be an important source of food during the early part of migration (Kristensen 1984, Svärdson et al. 1985). This was also reflected in the observed migration speed were we observed a greater migratory speed in smolts from Kärraån in the inner part of the fjord (Fig. 6 in **Paper IV**). Hence, it seems that smolts from Bodeleån utilize the feeding ground outside the river mouth before moving outwards in the fjord, whereas smolts from Kärraån quickly leave this area to find other feeding grounds.

Genetic population structure of sea trout (Paper V)

By collecting genetic samples of returning spawners from 20 rivers on the west coast of Sweden we aimed to determine the genetic structure of sea trout populations. More specifically we wanted to assess if genetic structure was mainly characterized by strong differentiation among individuals river population or in a hierarchical structure with close relationships between adjacent river populations. We found that sea trout show a hierarchical genetic structure, with neighbouring population forming distinct groups (Fig. 2 in **Paper V**). We also wanted to evaluate if angler caught sea trout came from local populations. Our results suggest the presence of nine genetic clusters (angler and sampled populations) on the west coast, where the river populations represent four main clusters. The five clusters not belonging to the river clusters can be explained either by intrusion of long distance migration of other populations or by artefacts occurring when the genetic material is of poor quality. However, most of the angler caught sea trout (72 %) came from local populations and only rod catches from the northern part of the coast displayed a higher degree of unassigned sea trout. It is therefore likely that these sea trout actually are migrants form e.g. Norwegian populations further north. These results suggest a large degree of straying or local adaptation to a broader geographical range rather than to a local river. This straying may be an adaptation for fishes spawning in small unpredictable streams with highly fluctuating discharge; i.e. that the trout stray because water levels are too low in their native stream.

General discussion and conclusions

Sea trout migration pattern in the sea has been given very little attention. My thesis can hopefully improve our current knowledge of sea trout migration and population dynamics using the west cost of Sweden as an experimental arena.

Migration patterns

In conclusion, this thesis found a large variation in migration tactics between years, rivers as well as within rivers (**Paper I, III and IV**). The environmental cues that trigger migration varied both between river and years; where migration was triggered by either temperature or discharge, or both (**Paper I**). This variation is in agreement with previous studies showing no conclusive results of the triggers, hence indicating local river specific responses to environmental cues (e.g. Jonsson and Ruud-Hansen 1985, Jonsson 1991, Hvidsten et al. 1995, Hembre et al. 2001). The river and estuarine migration however, was predominantly nocturnal which also has been detected in previous studies, thereby indicating a general pattern of migration (Thorpe et al. 1994, Moore and Potter 1994, Moore et al. 1998, Ibbotson et al. 2006, Aarestrup et al. 2014). The nocturnal migration is believed to be an anti-predator response as many predators are visual predators (**Paper I**). Here we demonstrate the novel finding that sea trout smolts form shoals with roach, a non-salmonid species (*R. rutilus*) during downstream migration, whereas previous studies only observed sea trout and Atlantic salmon forming shoals (Jonsson and Jonsson 2011). Although the sea trout adopts these tactics, mortality rates during river and early marine migration can be high, ranging between 5 and 51 % (**Paper III**). This paper further emphasizes the negative impact on sea trout populations by establishment of artificial ponds and wetlands which can cause substantial mortality rates (Jepsen et al. 1998, 2000, Olsson et al. 2001, Koed et al. 2006). We found that during years of low river discharge even the larger kelts suffered increased mortality rates compared to years with higher discharge. Downstream migration and consequently sea entry was found to occur in clusters (**Paper I, III and IV**).

The reason for the forming of theses clusters remains unknown, but is likely to be caused by differences in individual smoltification status (Björnsson et al. 2011), as growth rate and morphological characteristics failed to explain these differences (**Paper IV**). No similar findings have to my knowledge been observed previously in sea trout and this phenomenon clearly needs to be given further attention in the future.

In accordance with previous studies we found that migration speed decreases as the sea trout progressed towards the open ocean (Aarestrup et al. 2002, 2014, Thorstad et al. 2004, Finstad et al. 2005b). This lowered speed could be caused by several factors, but is most likely a consequence of the sea trout changing from navigation to foraging (**Paper III and IV**). Sea trout from both Bodeleån and Kärraån showed similar migration pathways and speed in the fjord (**Paper IV**), which goes in line with previous studies from Denmark (Aarestrup et al. 2014). This suggests that sea trout within a fjord system adopt similar migration tactics, which is logical as they are closely related and utilize the same environment within the sea (**Paper IV and V**). This does however need to be further investigated as there is a general lack of studies comparing migration tactics both within and between regions.

Population dynamics

Recruitment of brown trout on the west coast has remained stable (**Paper II**), though the effects of increased temperature on parr growth rate and smolt size, have led to larger yearlings and smaller smolts. This suggests that there is an increased selection for fast growth and that only a certain percent of the fastest growers are able to establish territories. This novel finding needs to be further evaluated and the consequences on life history traits and population structure in the future remain to be determined.

Future considerations

The variation in migratory tactics makes it difficult for stock managers to establish general regulations to conserve threatened populations in certain rivers. However, since my data suggest a limited number of related populations along the coastline (**Paper V**), it might not be necessary to manage all rivers within an area to the same extent since most of them resembles in their genetic constituents (**Paper V**). Nevertheless, the large variation in observed mortality rates between rivers indicates a need for individual based management (**Paper III and IV**). These mortality rates seem to be affected by the level of discharge in the system, where low discharge increases mortality (**Paper III**). In connection with future climate change the level of discharge may decrease even more leading to higher mortality rates in rivers especially in wetlands areas with a high abundance of predators. This highlights the need for more knowledge of the causes and consequences of early marine mortality and why loss rates vary between systems. Management actions needs to be taken to reduce mortality rates caused by anthropogenic disturbances such as wetlands, weirs and dams (Jepsen et al. 1998, Olsson et al. 2001, Koed et al. 2006, Gauld et al. 2013). Likewise, smaller smolts could lead to higher predation pressure as fewer predators should be gape limited (Skov et al. 2011). The consequences of a potential further decrease in smolt sizes still needs to be evaluated e.g. how population numbers are affected, but also if there are differences in the response depending on the habitat characteristics of the stream (for example, nutrient status, migratory distance and amplitude) as well as between the four genetic populations. Likewise we need to adapt the smolt production model (**Paper I**) to incorporate an increased amount of 1+ smolt scenario to increase the accuracy of the model, which otherwise is likely to underestimate the actual amount of smolts.

To conclude, the results presented here suggests that management actions should be taken on genetic cluster level (**Paper V**), whereas river based management within clusters should focus on larger stable systems that contribute to neighbouring smaller rivers with unpredictable flow regimes, as well as on individual rivers where survival bottlenecks (e.g. weirs, dams, wetlands etc.) are found (**Paper III and V**). In areas with many smaller streams (with various flow regimes), region specific management should be more successful. Further, a detailed genetic study (more rivers) needs to be undertaken on the west coast of Sweden in order to investigate the presence of additional possible clusters (similar to Sörån and Krokstrandsbäcken, **Paper V**) within the two larger clusters.

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