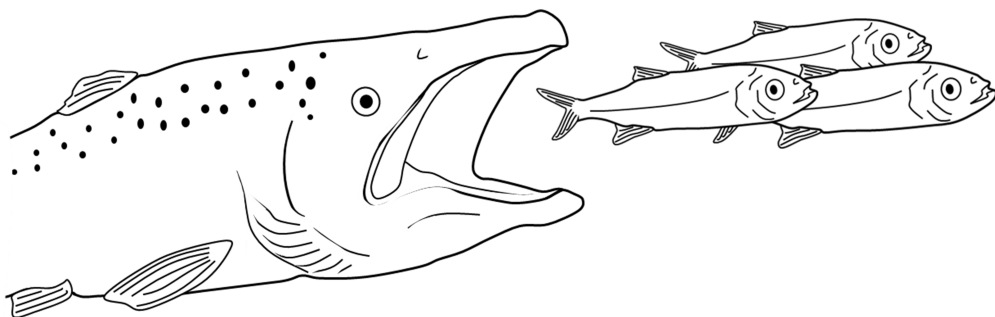




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Size-dependent predator-prey interactions, distribution and mortality in salmon: effects on individuals and populations

PHILIP JACOBSON



Size-dependent predator-prey
interactions, distribution and mortality in
salmon: effects on individuals and
populations

Philip Jacobson

*Faculty of Natural Resources and Agricultural Sciences
Department of Aquatic Resources
Öregrund*

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Abstract

The biomass dynamics of populations is largely determined by the survival, growth, and reproduction of individuals. For fish and other animals, survival, growth, and reproduction depends on the amount of energy an individual obtains via feeding and are therefore food-dependent. As fish often consume whole prey, the potential for a fish to consume prey depends on both its own size and the size of the prey. Furthermore, predation requires that the predator and prey overlap in time and space.

Anadromous fish are born in rivers, grow large at sea and return to rivers to spawn. Consequently, anadromous fish populations will be affected by size- and food-dependent processes in the river and at sea. However, we have limited knowledge about the importance of these processes at sea for the dynamics of anadromous fish. Therefore, the objective of this thesis was to assess whether and when size- and food-dependent processes at sea are important for anadromous fish dynamics. I approached this knowledge gap using empirical and theoretical methods with Atlantic salmon, *Salmo salar*, in the Baltic Sea as my study species.

I show that the diet of salmon at sea depends on their body size, the prey community size-structure and where salmon feed at sea, which, in turn, is governed by their body size and population-of-origin. The body condition of salmon at sea increased with prey availability at low prey densities. Moreover, growth and survival at sea differed between salmon originating from different rivers and inter-annual growth variation at sea contributed to explain inter-annual variation in the reproductive potential of salmon populations. I further show that the responses of anadromous fish populations to changes in river productivity and mortality targeting adults depend on if individuals compete for resources at sea or not and on sea productivity.

In summary, these findings demonstrate the importance of accounting for size- and food-dependent processes at sea, such as survival, growth, and size-dependent predator-prey interactions to increase our understanding of anadromous fish populations and how they will be affected by external drivers such as environmental change and fisheries.

Keywords: Anadromy, habitat shifts, population dynamics, prey availability, salmon, size-dependent predator-prey interactions, size-structure, spatial distribution.

Author's address: Philip Jacobson, SLU, Department of Aquatic Resources, Institute of Coastal Research, Skolgatan 6, 742 42, Öregrund, Sweden.

Storleksberoende artinteraktioner, utbredning och mortalitet hos lax: effekter på individer och populationer

Sammanfattning

Populationers biomassadynamik styrs främst av individers förmåga att överleva, växa och reproducera sig. Hos fisk och andra djur beror överlevnad, tillväxt och reproduktion på mängden energi en individ kan tillgodogöra sig via sin föda och dessa processer är därför födoberoende. Eftersom fisk oftast konsumerar sina byten hela, styrs deras möjlighet att konsumera byten av både sin egen och av bytets kroppsstorlek. Dessutom kräver predation att predatorer och bytesdjur överlappar i tid och rum.

Anadroma fiskar föds i sötvatten, växer sig stora till havs och återvänder till sötvatten för att reproducera sig. Således kommer anadroma fiskpopulationer att regleras av storleks- och födo-beroende processer både i sötvatten och till havs. Trots detta har vi idag mycket begränsad kunskap om storleks- och födoberoende processer till havs för att förstå dynamiken hos anadrom fisk. Målsättningen med denna avhandling var därför att undersöka om och när storleks- och födoberoende processer till havs är viktiga för dynamiken hos anadrom fisk. För att fylla denna kunskapslucka har jag använt mig av empiriska och teoretiska metoder med Atlantlax, *Salmo salar*, i Östersjön som min studieorganism.

Jag visar att laxens diet till havs beror på dess kroppsstorlek, bytessamhällets storleksstruktur och var laxen äter till havs, vilket i sin tur styrs av dess storlek och vilken älv den kommer ifrån. Dessutom ökade kroppsconditionen hos lax till havs med bytestillgänglighet vid låga bytestätheter. Tillväxt och överlevnad till havs skiljde sig mellan laxar som härstammar från olika älvar och mellanårsvariation i tillväxt till havs bidrog till att förklara mellanårsvariation i laxpopulationers reproduktionspotential. Utöver detta visar jag att anadroma fiskpopulationer svarar olika på förändringar i älvproduktivitet och dödlighet beroende på huruvida individer konkurrerar om föda till havs eller inte och beroende på havets produktivitetsnivå.

Sammanfattningsvis visar mina resultat att storleks- och födoberoende processer till havs, så som överlevnad, tillväxt och storleksberoende artinteraktioner, är viktiga att ta hänsyn till för att öka vår förståelse om populationsdynamiken hos anadrom fisk och hur de kan komma att svara på förändringar i miljön och andra påverkansfaktorer såsom fiske.

Nyckelord: Anadromi, habitat-skiften, populationsdynamik, bytestillgänglighet, lax, storleksberoende artinteraktioner, storleksstruktur, rumslig utbredning.

Författarens adress: Philip Jacobson, SLU, Institutionen för akvatiska resurser, Kustlaboratoriet, Skolgatan 6, 742 42, Öregrund, Sverige.

Dedication

To Emelie and Bonnie.

The water you touch in a river is the last of that which has passed, and the first of that which is coming; thus it is with time.

Leonardo da Vinci.

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List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

- I Jacobson, P*., Gårdmark, A., Östergren, J., Casini, M., Huss, M. (2018). Size-dependent prey availability affects diet and performance of predatory fish at sea: a case study of Atlantic salmon. *Ecosphere*, 9 (1), pp. e0208.
- II Jacobson, P*., Gårdmark, A., Huss, M. (2020). Population and size-specific distribution of Atlantic salmon *Salmo salar* in the Baltic Sea over five decades. *Journal of Fish Biology*, 96, pp. 408-417.
- III Jacobson, P*., Whitlock, R., Huss, M., Leonardsson, K., Östergren, J., Gårdmark, A. Growth variation of Atlantic salmon, *Salmo salar*, at sea affects their annual roe production. (Submitted manuscript)
- IV Jacobson, P*., Gårdmark, A., Östergren, J., Huss, M. Stage-specific biomass responses to shifts in habitat productivity and mortality in anadromous fish varies with density dependence at sea. (manuscript)

Paper I and II are open access publications (CC BY 3.0 and CC BY 4.0).

* Corresponding author.

The contribution of P. Jacobson to the papers included in this thesis was as follows:

- I Participated in the planning of the study, assembled the data and conducted the statistical analyses. Led the writing and created all graphic content of the article. Handled the review process.
- II Participated in the planning of the study, assembled the data and conducted the statistical analyses. Led the writing and created all graphic content of the article. Handled the review process.
- III Participated in the planning of the study, gathered and assembled the data and conducted the statistical analyses. Led the writing and created all graphic content of the manuscript.
- IV Participated in the planning of the study and model design. Parameterized the model and conducted model analyses. Led the writing and created all graphic content of the manuscript.

1 Introduction

Two processes govern the biomass dynamics of closed populations: biomass production and biomass loss. Biomass is produced via reproduction and growth and is lost via metabolic costs and death. Reproduction, growth, metabolism, and death occur at the biological scale of individuals. For fish, growth is food-dependent and their metabolism and fecundity depends on their body size, and since feeding is a size-dependent process, they are indirectly food-dependent. Thus, the dynamics of populations are governed by size- and food-dependent processes occurring at the biological scales of individuals.

1.1 Size-dependencies of biomass production

Like most organisms, fish develop over life before reproducing. As they develop, they can grow several orders of magnitude in body size (Werner and Gilliam 1984). In addition, fish are known to display indeterminate growth, meaning that individuals continue to grow throughout their life (Sebens 1987). Fish are also heterotrophic organisms as they rely on feeding on other organisms to grow, store energy, reproduce, and to avoid starvation and ultimately death. Therefore, the ontogenetic development of fish, as well as their possibility to store energy and reproduce, will depend on their success in requiring energy via feeding.

1.1.1 Size-dependent feeding

Predatory fish consume whole prey items (Mittelbach and Persson 1998, Scharf et al. 2000). This means that the size of consumable prey items will depend on the gape-size of the predator. Therefore, the amount of prey that a predator can consume depends on both the size of the predator and the prey. As predatory fish

grow they incorporate larger prey items in their diet, increasing the size-range of potential prey as they grow in size (Scharf et al. 2000, Gaeta et al. 2018, Jacobson et al. 2019). However, body size is not the only factor that determines the predators' success in feeding. The predator and prey also need to overlap in time and space for consumption to be possible. Therefore, differently sized predators within a population, despite occupying the same space, can have access to different amounts of consumable prey and equally sized predators can experience different prey availabilities if they occupy different feeding areas.

1.1.2 Size-dependent reproduction

After a fish has reached sexual maturation, the available energy gained via feeding after covering maintenance costs (such as metabolism and cell renewal), can either be spent on growth, energy storage, or gonad production. Fecundity, the total egg production of an individual, increases with body size for female fish as they can produce larger gonads due to a larger body. However, there is a trade-off between spending surplus energy into growth (which would make it possible to develop larger gonads in the future) or directly invest surplus energy into gonad production (Heino and Kaitala 1999). Irrespectively of whether a fish chooses to invest surplus energy in gonad development or increased growth, the success in either of these strategies is food- and size-dependent.

1.2 Size-dependencies of biomass loss

1.2.1 Size-dependent survival

Given that only a minor part of all fertilized eggs survives and reaches sexual maturation (egg-to-adult mortality often exceeds 99%), a living adult fish can be viewed as an exception (Dahlberg 1979, Viljanen and Holopainen 1982). The highest mortality rates occur in early developmental stages (Dahlberg 1979, McGurk 1986, Lorenzen 1996). In temperate regions, size further influences the capability of an individual to store energy used to endure and survive long periods without feeding such as winter periods (Post and Evans 1989, Huss et al. 2008). In addition, predation pressure is higher on small compared to large fish, as smaller fish can be consumed by more predators than large and large fish have a greater potential to actively avoid predators (Lundvall et al. 1999, Nilsson and Brönmark 2000, Scharf et al. 2000). Consequently, their survival is both food- and size-dependent.

Fisheries-induced mortality differs from natural mortality as it often targets and kills large individuals within a population due to the usage of size-selective fishing gear (Hamley 1975, Løkkeborg and Bjordal 1992, Sala et al. 2008). Size-selective fisheries targeting large individuals in a population can truncate the size and age-distribution of the fish population (Beamish et al. 2006, Stewart 2011) and induce evolutionary shifts in e.g. growth and size-at-maturation (Kuparinen and Merila 2007, Swain et al. 2007). Given that natural and fisheries mortality affect differently sized individuals, changes in such size-selective mortality can have a large impact on the whole population, as size-selective mortality can induce shifts in size-structure and population dynamics (Persson et al. 2007, van Kooten et al. 2007, Ohlberger et al. 2011).

1.2.2 Size-dependent metabolism

For fish, the total energy demand needed for maintaining body functions, i.e. metabolism, increases as it grows in body mass in an allometric fashion. In other words, the increase is non-linear and increases with an exponent <1 (Clarke and Johnston 1999, Brown et al. 2004), meaning that the metabolic cost per unit biomass decreases with increased body size. Consequently, if a fish has a constant energy intake while growing, the amount of surplus energy available to invest in either growth, energy storage or reproduction will eventually decrease with increased size and become ≤ 0 , leading to ceased growth, starvation and ultimately death (Werner and Gilliam 1984). However, as individuals grow they can shift prey types and feed on larger and more energy-rich prey, such as switching from zooplankton and benthic invertebrates to fish (becoming piscivorous; Mittelbach and Persson 1998), to compensate for the increased metabolic demands of a larger body, a phenomenon known as ontogenetic niche shifts (Werner and Gilliam 1984, Miller and Rudolf 2011).

1.3 Ontogenetic niche shifts

Ontogenetic niche shifts occur as a response to ontogenetic development as fish often need to switch prey types to cope with increased maintenance costs associated with a larger body. For fish to access new prey types (e.g. a shift from benthic invertebrates to fish), they often need to shift habitat (Werner and Gilliam 1984, Olson 1996, Mittelbach and Persson 1998, Svanbäck and Eklöv 2002). However, habitat shifts can also lead to higher predation risk, inducing a trade-off between increased growth rate and increased predation risk (Werner and Hall 1988, Dahlgren and Eggleston 2000). For species characterized by ontogenetic niche shifts, accounting for individual-level processes in all habitats

utilized over life is important to understand their population dynamics, as changes occurring in one habitat can affect individuals in other habitats and therefore also the population as a whole (de Roos et al. 2008a, van de Wolfshaar et al. 2011, Schröder et al. 2014, Reichstein et al. 2015). However, these findings are mainly based on theoretical studies with some support from experiments and observation data in small and enclosed aquatic systems (Persson et al. 2007, Schröder et al. 2009, Ohlberger et al. 2011, Reichstein et al. 2015). Thus, observational studies assessing whether size- and food-dependent individual-level processes are important to consider for understanding the dynamics of populations characterized by ontogenetic niche shifts in large and open systems are largely lacking (but see Gårdmark et al. 2015).

1.4 Anadromous fish populations

Anadromous fish display habitat shifts over their lifetime as they are born in freshwater, migrate to brackish or marine systems, and later return to freshwater to spawn. Consequently, individuals within the same population can occupy very different environments, feeding in either a river or at sea. Several of the most recognized examples of anadromous fish species are found within the family Salmonidae, including pacific salmon species (*Oncorhynchus* spp.) and Atlantic salmon (*Salmo salar*) (Klemetsen et al. 2003, Quinn and Myers 2005).

The life-cycle of anadromous Atlantic salmon includes habitat shifts (Fig. 1). Atlantic salmon develop through several life-stages in the river, known as alevin, fry, parr, and smolt (Fig. 1). When an individual transitions into the smolt life-stage, it becomes silvery and starts to swim with the current towards the river mouth to eventually reach the sea. Once at sea, salmon feed and grow for one to several years before they return to their natal river to mature and spawn (Erkinaro et al. 2019). This happens in most cases, but straying (i.e. salmon spawning in another river than its natal river) does occur (Vasemägi et al. 2005, Palmé et al. 2012). Also, most salmon die after spawning, although some (primarily females) survive and can spawn more than once during life (known as kelts) (Lundqvist et al. 2015, Erkinaro et al. 2019). Regarding the dynamics of Atlantic salmon populations, density-dependent processes in the river habitat (i.e. competition for resources among juveniles) and how this affects and limits the population size has been intensively studied (e.g. Jonsson et al. 1998, Einum et al. 2006, Aas et al. 2011). Due to this density-dependency, the population size of Atlantic salmon populations is commonly regarded to be determined by the carrying-capacity of juveniles in the river habitat, setting the upper limit of the amount of smolt that annually leaves the river. The amount of smolt that leave the river will govern the upper limit of returning adults, which in turn governs

the reproductive potential of the population. However, despite that juvenile and adult life-stages of Atlantic salmon have been extensively studied over the past decades (Fleming 1996, Klemetsen et al. 2003, Aas et al. 2011), we still have limited knowledge about factors affecting the growth, energy storage and survival of individual salmon at sea and how variation in these processes could affect the population as a whole (Chaput 2012, Friedland et al. 2014, Soto et al. 2018).

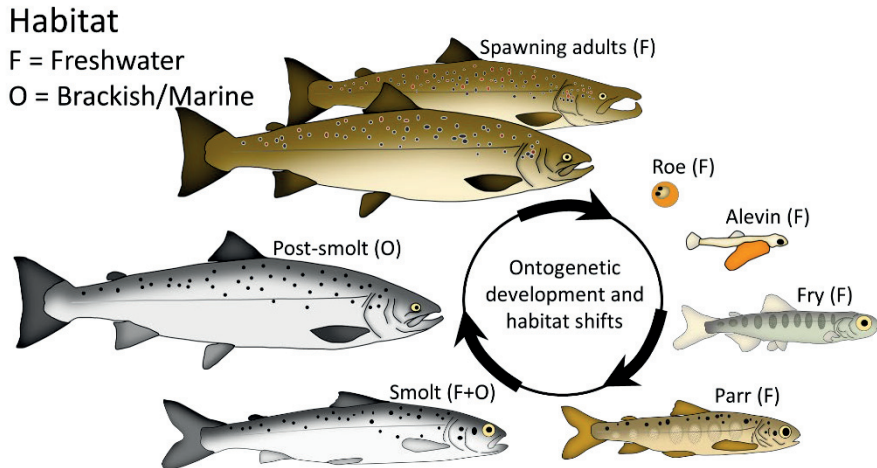


Figure 1. The generalized life-history of anadromous Atlantic salmon showing its developmental life-stages and associated habitats. Repeated spawners (kelts) and pre-mature spawning male parr are not shown in this generalized life-history.

1.4.1 Atlantic salmon at sea

Compared to the amount and detailed knowledge regarding the freshwater life-stages of Atlantic salmon, we know little about the factors and processes that affect individuals during their time spent at sea (Klemetsen et al. 2003, Aas et al. 2011, Chaput 2012, Friedland et al. 2014, Soto et al. 2018). During recent decades, many salmon populations have shown negative trends in abundance despite decreased fisheries at sea and improvements of spawning and juvenile habitats (Chaput 2012, Soto et al. 2018). As suggested by Chaput (2012) and Soto et al. (2018), other factors than fisheries mortality affecting salmon at sea likely contribute to these wide-spread declines. For salmon originating from rivers connected to the Baltic Sea, many populations have shown positive trends in abundance since the 1990s and many populations have reached management targets, most likely due to reduced mixed-population fisheries at sea (Karlsson

and Karlström 1994, ICES 2019). However, not all populations have responded equally and there are still some that show no, or even negative trends in abundance since the 1990s, for reasons that are poorly understood (ICES 2019). Put together, these studies suggest that other factors at sea than decreased mortality can affect the dynamics of Atlantic salmon populations. Assessing factors causing variation in individual-level processes and characteristics at sea (such as survival, body condition, and growth) and, in turn, how variation in these processes and characteristics affects the dynamics of salmon populations could be one step towards improving our understanding of the dynamics of Atlantic salmon populations specifically, and also of anadromous fish populations generally.

2 Goals of this thesis

The goal of this thesis was to study, using empirical and theoretical approaches, whether and when size- and food-dependent individual-level processes at sea are important to consider to understand the dynamics of Atlantic salmon populations. More specifically, I ask the following questions in my thesis:

Do diet and body condition of salmon at sea depend on size-specific prey availability? (**Paper I**)

Is the distribution of salmon at sea size-dependent and does it differ among populations? (**Paper II**)

Is growth at sea important to consider for understanding inter-annual variation in the reproductive potential of Atlantic salmon populations? (**Paper III**)

How does density-dependence at sea shape population responses to changes in habitat-specific productivity and adult mortality in anadromous fish? (**Paper IV**)

3 Material and Methods

To assess whether and when size- and food-dependent individual-level processes at sea matter for the dynamics of anadromous fish populations, I have used both empirical and theoretical approaches. **Paper I-III** are empirical studies, based on large datasets collected before this PhD project started (Table 1). **Paper IV** is a theoretical study, in which I use a dynamic stage-structured biomass model (de Roos et al. 2008b). Below, I provide more detailed information regarding my study system, study species and the empirical and theoretical approaches I have used in this thesis.

3.1 Study system

3.1.1 The Baltic Sea

The Baltic Sea is one of the largest brackish water bodies on earth. It is a semi-enclosed and shallow sea with more than one-third of its surface being less than 30 meters deep. The Baltic Sea is connected to the North Sea via narrow and shallow straits between Sweden and Denmark (HELCOM 2018). Due to these narrow and shallow straits, the water exchange of the Baltic Sea is slow, and a complete exchange takes 25-30 years. The salinity levels in the Baltic Sea decrease with increased distance from the shallow and narrow straits in the south and varies from ~15 PSU close to the straits to 0-3 PSU in the northern parts (HELCOM 2018). This salinity gradient affects the species composition of the Baltic Sea, where marine species dominate in the south while freshwater species dominate in the north, although many marine and freshwater species overlap spatially in large parts of the Baltic Sea (Bonsdorff 2006, Gogina and Zettler 2010, Vuorinen et al. 2015).

Around 85 million people are living around the Baltic Sea in nine different countries (HELCOM 2018). Since the 1950s, nutrient loadings from these countries to the Baltic Sea increased and peaked in the 1980s after which the input has decreased (Reusch et al. 2018). Despite this decrease in nutrient input, eutrophication is still of major concern in the Baltic Sea region (HELCOM 2018). In addition to nutrients, the input of persistent organic pollutants (POPs), such as hazardous dioxins and PCBs, increased in the 1960s and reached high concentrations in the Baltic Sea, causing severe reproductive disorders in several top-predators, such as seals and eagles (Helle et al. 1976, Helle 1980, Miller et al. 2014, Bignert et al. 2015, Nyberg et al. 2015). Despite declining trends in the concentration of many different pollutants during recent years, various pollutant concentrations in biota, and especially in fatty fish such as herring and salmon, often exceed limits set for human consumption (Bignert et al. 2017, ICES 2019).

3.1.2 Baltic salmon

The species which I have primarily studied in this thesis is the anadromous Atlantic salmon (*Salmo salar*) originating from rivers connected to the Baltic Sea (hereafter referred to as Baltic salmon) (Verspooor et al. 2007). In addition to Baltic salmon, I have also studied its main prey species at sea, herring (*Clupea harengus*), sprat (*Sprattus sprattus*) and three-spined stickleback (*Gasterosteus aculeatus*) (Karlsson et al. 1999, Hansson et al. 2001). Historically, ~100 distinct Baltic salmon populations spawned in rivers connected to the Baltic Sea (Karlsson and Karlström 1994). During the 20th century, the amount of self-sustained Baltic salmon populations decreased due to the development of hydro-power plants. Today, 27 Baltic salmon populations are classified as being wild and self-sustaining populations (ICES 2019). Also, 31 populations either rely partly or completely on releases of reared salmon to avoid extinction, classified as mixed or reread populations respectively (ICES 2019). 4-6 million hatchery-reared smolts are released annually in the Baltic Sea region (ICES 2019). All hatchery-reared salmon in Sweden are marked before release via removal of their adipose fin, making it possible to visually assess their origin (i.e. wild [adipose fin present] or reared [adipose fin absent]). During the last decade, the amount of wild Baltic salmon has generally increased due to decreased fishing at sea, which targeted salmon from many different populations due to mixing while feeding out at sea (Ikonen 2006, ICES 2019). Not only has the commercial fisheries decreased, but it has also moved from offshore areas towards the coast and into rivers, targeting salmon on their spawning migration towards their natal river and also in their natal river (ICES 2019). As shown by Whitlock et al. (2018), the closer fishing is conducted to a specific river mouth, the larger

proportion of the catch will originate from that river. However, some nations (Denmark and Poland) still conduct mix-population fishing at sea, mainly in the most southern parts of the Baltic Sea (ICES 2019).

Status of Baltic salmon populations

Despite the positive development of many (but not all) wild Baltic salmon populations during the last decade, other challenges not related to fisheries are present. Two of these are the reproductive disorder syndrome called M74 (Bengtsson et al. 1999, Mikkonen et al. 2011, Keinänen et al. 2012, ICES 2019) and disease outbreaks visually evident via external infections and fungi, killing adults in the rivers before spawning (ICES 2019). The M74 syndrome is a syndrome associated with a high mortality of fertilized eggs and alevins (life-stages before external feeding is initiated) (Fig. 1). During these early life-stages, survival and development are dependent on the yolk-sac which contains all vital substances required by the juvenile to survive. However, for females affected by the M74 syndrome, there is a vitamin shortage in the yolk-sac, associated with the high mortality of their offspring. The M74 syndrome can be reversed by treatment with thiamine (vitamin B₁), either via bathing of fertilized roe or injection in adult females before spawning (Bengtsson et al. 1999, ICES 2019). As thiamine is a vitamin, salmon cannot produce it by themselves, but instead, they need to acquire it while feeding at sea (Keinänen et al. 2012, 2017, 2018). The more recent disease outbreaks, where adult salmon have been found dead in rivers with severe external infections and fungi before spawning, have been observed in some but not all Baltic salmon populations. The first concerns regarding these disease outbreaks were raised in 2014-2015 (ICES 2019), and the outbreaks have since then varied in severity within and among populations. Currently, we do not know why these salmon die before spawning nor why only some populations are affected by these diseases outbreaks but this health issue likely stems from processes occurring at sea (ICES 2019).

3.2 Empirical approaches

In this thesis, I have used several independent and large data sets covering both individual- and population-level aspects of Baltic salmon at sea (Table 1). The salmon diet database contains data on the stomach content of salmon at sea, captured in 1959-1962 and 1994-1997 (Karlsson et al. 1999, Hansson et al. 2001). This dataset was used in **Paper I** to *i*) compare the diet of salmon at sea on a finer spatial scale than in previous studies, *ii*) calculate the predation window of salmon at sea (the size-ratio between salmon and their prey) and *iii*)

to compare the diet with the prey community using spatially resolved size-distribution data of the fish prey community in overlapping years (BIAS dataset, Table 1). I also combined the derived predation window of salmon with the BIAS data to estimate the size-specific prey availability of differently sized salmon in different regions of the Baltic Sea for the time period 1984-2015.

In **Paper II**, I used the Carlin-tagging recapture database to assess the distribution of salmon at sea for salmon originating from ten different rivers. This database contains recapture locations of recaptured and reported Carlin-tagged (which are unique external tags) salmon at sea caught 1951-1999 (Table 1). Using this data, I assessed the distribution patterns among populations, how it varied among year-classes and how the distribution varied among individuals within year-classes. As I have not found data on the effort and spatial distribution of commercial fisheries targeting salmon at sea on a matching spatial scale with the Carlin-recapture data for the time-period 1951-1999, I compared distribution differences among and within populations for similar-sized salmon and time-periods, and not how the distribution of salmon at sea changed over time. This is because it is impossible to disentangle differences in distribution over time without accounting for the non-random effort and distribution of commercial fisheries, as salmon can distribute into regions where no fishing was conducted and fishing effort will affect the probability of catching a tagged salmon.

The Carlin-tagging recapture database was also used in **Paper III** to calculate population- and size-specific growth rates at sea for salmon originating from two populations (Dalälven and Umeälven) and as input in a Bayesian mark-recapture model (Whitlock et al. 2016), used for estimating their mortality rates at sea (both natural and fisheries mortality). In addition to growth and survival at sea, I used records on the annual numbers of released smolts in my two study populations (Table 1). The size-specific growth, population-specific survival at sea estimates, and the annual number of released smolts were used to test whether inter-annual growth variation at sea increased the explanatory power of the variation in the inter-annual roe production in the study populations. The annual potential roe production was calculated using data covering numbers, body size and sex of the annual spawning run in both Dalälven and Umeälven, in combination with size-specific fecundity data from the hatchery in river Dalälven (Table 1).

Table 1. Summary and description of the datasets used in this thesis.

Data set	Contains	Temporal coverage	Usage	Note
Salmon diet database	Length, weight and stomach content data of >8000 individual salmon captured at sea.	1959-1962, 1994-1997	Paper I – Used for estimating the predation window of salmon at sea and for comparing observed diet with available prey.	Previously published data (Karlsson et al. 1999, Hansson et al. 2001).
Baltic Integrated Acoustic Survey (BIAS)	Spatially resolved data on biomass and length distributions of sprat and herring in the Baltic Sea, retrieved from the annual Baltic Integrated Acoustic Survey (BIAS).	1984-2015	Paper I –Used for calculating spatially resolved prey availability estimates for salmon at sea.	For more information about this survey see ICES (2016).
Carlin-tagging recapture data	Length at tagging, time of release (day, month and year), place of release and population of origin. Time of recapture (day, month, year), recapture location, length and weight at recapture, fishing gear type, and nationality of fisher. >120 000 recaptures.	1951-1999	Paper II – Size-and population-specific distribution of salmon at sea. Paper III - Population- and size-specific growth at sea. Estimating population-specific survival rates at sea.	Parts previously published in (Larsson 1984, Petersson et al. 1996).
Annual releases of smolt individuals	Population-specific amount of annually released salmon smolts.	1866-2015	Paper III – Used for estimates on annual differences in smolt-year class size in statistical analyses.	Unpublished report by Östergren and Persson (In prep).
Annual spawning run data for Dalälven and Umeälven	Annual amount of returning males and females and their lengths and weights.	1960-2019	Paper III – Used for calculating the potential population-specific annual roe production for salmon originating from Dalälven and Umeälven.	Annually monitored in Dalälven and Umeälven.
Female salmon fecundity data from river Dalälven	Produced roe biomass of different sized salmon females. >1400 females	2004-2016	Paper III – Used for converting salmon female size to roe biomass.	Data acquired from the broodstock facility in Dalälven.

3.3 Theoretical approaches

Theoretical approaches in ecology are powerful and efficient for identifying and investigating key mechanisms affecting the dynamics of populations. This is especially true for populations characterized by long-lived individuals, which are distributed over large areas over life, as planning and conducting experiments on large temporal and spatial scales would be extremely resource and time-demanding. Therefore, I used a theoretical approach to assess how habitat-specific changes in productivity and adult mortality affected the biomass dynamics in anadromous fish populations displaying varying density-dependencies at sea. This was done by altering resource competition within and between life-stages feeding at sea (**Paper IV**). I used a dynamic stage-structured biomass model (de Roos et al. 2008b, de Roos and Persson 2013), which is based on individual energetics and food-dependent development and allows for separating the population into distinct life-stages. The emerging population dynamics are determined by individual-level food- and size-dependent processes (ingestion rates, metabolic costs, survival and growth) within each life-stage of the population. Thus, this model framework was highly suitable for assessing how varying density-dependent feedbacks at sea affects the responses of anadromous fish populations to habitat-specific changes in productivity and mortality.

4 Results and Discussion

4.1 Size-specific predator-prey interactions and food-dependent body condition of salmon at sea (Paper I)

I show that accounting for the size of both salmon and its prey is important for understanding the diet composition of salmon and the amount of prey that salmon can consume at sea. As salmon increase in body size, they incorporate larger prey while still feeding on small prey, widening the size range of consumed prey as they grow at sea (similar to many other piscivorous fish (Scharf et al. 2000, Gaeta et al. 2018, Jacobson et al. 2019)). The amount of consumable prey for equally sized salmon varied among regions in the Baltic Sea. In addition, due to the size-dependent interactions between salmon and their prey, the amount of consumable prey within regions differed among differently sized salmon. I further show that at low levels of available and consumable prey, the body condition of salmon increased with increased prey availability. However, at high levels of available and consumable prey, this relationship was not evident as body condition was unaffected by an additional increase in prey. Importantly, this relationship was not evident when ignoring the size-dependency of the interaction between salmon and their prey at sea. These novel findings suggest that the body condition of salmon can be resource-limited at sea, a limitation only possible to identify when accounting for the size-dependency of the interaction between salmon and its prey.

4.2 Size- and population-specific distribution of salmon at sea (Paper II)

In **Paper II**, I show that the distribution of salmon at sea depends on their body size and that this size-dependency varies among populations. I further show that the variation in distribution at sea within smolt year classes (individual-level variation in distribution) was higher in some populations compared to in others. Combined, these results show that salmon at sea can experience different environments depending on their size and from which population they originate. In addition, individuals within the same year class can experience more or less similar environments at sea depending on from which population they originate. This is evident when combining the results in **Paper I** and the results in this study, showing that equally sized salmon at sea from different populations do experience different prey availabilities, both in terms of prey species and consumable prey biomass (Fig. 2, differences between panels). Also, salmon within the same smolt year class within a population can either experience similar amounts of consumable prey or not, depending on population-of-origin

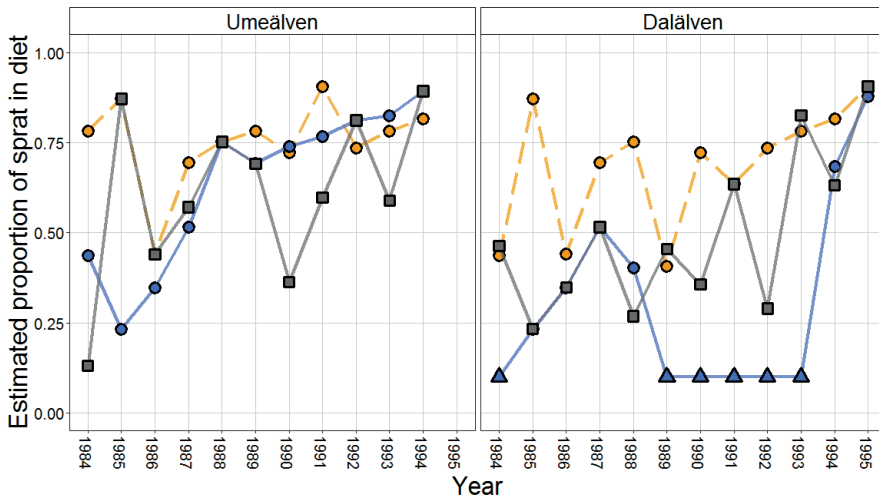


Figure 2. Estimated proportion of sprat biomass in the diet of a 60 cm salmon originating from river Umeälven (left) and Dalälven (right), based on their distribution at sea, size-specific feeding and annual size- and area-specific prey (herring and sprat) availability in different parts of the Baltic Sea, for the years with recapture data in the time-period 1984–1995. Grey squares (solid line) show estimates based on the annual mean recapture latitude of 50–70 cm salmon, while yellow and blue dots show estimates based on the 25th (yellow dots, dashed line, south of the mean) and the 75th (blue dots, solid line, north of the mean) percentile of the annual recapture latitude, respectively. If the recapture latitude was above 60.5°N, i.e. in the Bothnian Sea or Bothnian Bay in the northern Baltic Sea, we assumed that sprat constituted 10% of the diet biomass composition (triangles) due to a lack of prey availability data in this area (**Paper I**).

(Fig. 2, cf. differences between lines within panels). These findings could be important to consider as differences in prey availability at sea can affect the body condition of salmon at sea (**Paper I**). In addition, the results in this study could potentially contribute to understanding why some populations are more affected by the M74 reproductive syndrome and the recent disease outbreaks than others (Keinänen et al. 2012, Keinänen et al. 2018, ICES 2019). Furthermore, the current Baltic salmon assessment assumes that all Baltic salmon populations will show identical responses to changes in fisheries at sea. However, the nations that are fishing for salmon at sea conduct their fishing in the southernmost regions of the Baltic Sea (ICES 2019), and the populations characterized by feeding in the southern parts of the Baltic Sea (e.g. Umeälven and Mörrumsån) are likely the ones being affected by changes in current fisheries at sea. Thus, our novel findings in **Paper II** questions the current assessment assumption that all salmon populations will respond identically to changes in fisheries at sea.

4.3 Effects of growth variation at sea on the annual roe production of salmon (Paper III)

In this study, I show that size-specific growth at sea, in combination with survival at sea and smolt year class abundance, adds to explain inter-annual variation in the potential roe production of Baltic salmon. However, this relationship between growth at sea and inter-annual variation in potential roe production was only evident in one of our study populations (in the population originating from Dalälven, not in Umeälven). Thus, in some populations, variation in growth at sea can affect the annual reproductive potential of the population. This finding suggests that inter-annual variation in growth at sea, which is an individual food- and size-dependent process, can be important to consider for understanding annual fluctuations in salmon population densities, as the reproductive potential of the population sets the upper limit of the population size. Why this relationship between growth variation at sea and reproductive potential was not evident in both our study populations could be due to differences in data coverage between our two study populations. It could also be that growth variation in Umeälven does not affect the reproductive potential as much as survival at sea or smolt year class abundance does, while growth might have a larger impact in Dalälven. In addition to these main findings of this paper, I also found that growth and survival at sea were not identical among salmon from Dalälven and Umeälven. Given the results in **Paper I** and **II**, these findings further indicate that salmon from different populations experience different environments while feeding at sea, affecting their performance.

4.4 Anadromous population responses to habitat change are determined by density-dependent resource feedbacks at sea (Paper IV)

The main finding in this study is that different types of feedbacks between consumers (e.g. a salmon) and their resource (e.g. a herring) at sea determines how anadromous fish populations respond to habitat-specific changes in river productivity and mortality targeting adult consumers. For example, in the model scenario where juvenile and adult consumers compete for resources at sea, increased adult mortality led to an initial increase (followed by a decrease) in the total biomass of the population (known as overcompensation) (de Roos et al. 2007, Schröder et al. 2009, Reichstein et al. 2015). Also, increased river productivity led to a linear increase of biomass in all life-stages when adults did not feed and juveniles at sea did not affect their resource, mimicking Atlantic salmon feeding patterns (Jonsson et al. 1998). However, when juveniles compete for resources at sea among themselves, the response of the population to increased river productivity became non-linear and differed among life-stages. In addition, productivity at sea also affected how the population responded to increased river productivity and increased adult mortality. Therefore, to understand how an anadromous fish population will respond to habitat-specific changes, such as river productivity and adult mortality, knowledge of food-dependent processes and resource competition at sea, in combination with productivity levels at sea, is important. These findings suggest that the inclusion of data regarding the abundance and management of prey fish at sea could be important when planning, and to accurately predict, the effects of conservation and management actions targeting anadromous fish populations, such as river restorations and fishing regulations.

5 Conclusions and future perspectives

The combined results presented in this thesis show that size- and food-dependent individual-level processes at sea and how these processes are affected by size-specific predator-prey interactions are important to consider to increase our understanding regarding the dynamics of anadromous fish populations (**Paper I, II, III**). Also, individual-level size- and food-dependent processes, such as growth, migration patterns, and survival can vary among individuals, both within but also among populations despite sharing the same sea (**Paper II, III**). Such variation in individual-level processes at sea among populations could be one reason why some populations show more similar dynamics than others and why some and not all Baltic salmon populations show similar M74 syndrome frequencies and disease outbreaks. Furthermore, the results in this thesis highlight the need for accounting for size- and food-dependent processes such as growth and feeding interactions at sea when studying how anadromous fish populations respond to environmental change, such as habitat-specific productivity, and changes in fisheries mortality (**Paper IV**).

I further show that despite originating from rivers connected to the same sea, individuals can experience very different environments within that sea and consequently respond differently to small-scale environmental changes. Given that many anadromous fish populations have declined in numbers during recent decades (e.g. Limburg and Waldman 2009), which can not only be explained by changes in fisheries mortality, river habitat quality and large scale climate fluctuations (Chaput 2012, Soto et al. 2018), accounting for size- and food-dependencies at sea, i.e. fundamental ecological processes, might help to understand these wide-spread declines. This is especially important now more than ever given that the world's oceans will change substantially in the near future due to climate change (IPCC 2019). Thanks to new technologies and methods, we have during the last decade increased our knowledge regarding the life of salmon at sea, including new insights about their distribution patterns (MacKenzie et al. 2012, Lacroix 2013, Strøm et al. 2018, Freshwater et al. 2019),

diet at sea (Dixon et al. 2017, Torniaainen et al. 2017, Keinänen et al. 2018), natural mortality at sea (Strøm et al. 2019) and how various salmon species potentially respond to climate change (Crozier and Hutchings 2014, Friedland et al. 2014, Soto et al. 2018, Cline et al. 2019). However, we still have a lot to explore, especially regarding the variability of the distribution, diet, growth, and survival of individuals at sea, if these processes differ systematically among populations (**Paper II** and **III**) and if such variability affects the dynamics of anadromous fish equally or not (**Paper III** and **IV**). Recent studies indicate that safe-guarding intra-specific variation in traits and distribution patterns at sea can be highly important to ensure population and community stability (Schindler et al. 2010, Des Roches et al. 2018, Freshwater et al. 2019). Thus, increased information regarding factors influencing individual-level size- and food-dependent processes and size-dependent predator-prey interactions for salmon and other anadromous fish at sea, and how these processes vary both within and among populations, is important for increasing our understanding of the dynamics of anadromous fish at present but also in changing environments.

The findings in this thesis further strengthen current arguments for developing a more population-specific management of salmon (e.g. Crozier et al. 2004, Whitlock et al. 2018), as salmon from different populations will be affected by environmental change and changes in fisheries at sea differently (**Paper I, II** and **III**). In addition, the results in this thesis further suggest that considering changes in abundance, size-structure, and distribution of prey fish at sea, using multi-species management approaches, could be needed for developing a more population-specific management of salmon as changes in size-dependent prey availability can affect the performance of salmon at sea and the biomass dynamics of salmon populations (**Paper I** and **IV**).

Accounting for shifts in the abundance and size-structure of salmon prey at sea could also be important for assessing management actions suggested to decrease concentrations of hazardous substances in salmon and their prey, such as increased fisheries (Parmanne et al. 2006, TemaNord 2010). Size-selective mortality (either via predation or fisheries) can shift the size-distribution and growth of salmon prey at sea (van Leeuwen et al. 2008, Sharpe and Hendry 2009, Huss et al. 2014, Östman et al. 2014) and thus alter the amount of available prey for differently sized salmon. As the content of hazardous and persistent substances, such as dioxins, in Baltic Sea herring and sprat (which is the main prey of salmon) increases with age, large herring and sprat will contain more dioxin than small (Vuorinen et al. 2002, Koistinen et al. 2008, Vuorinen et al. 2012). Consequently, as large salmon generally feed on larger herring and sprat compared to small (**Paper I**), changes in the size distribution of the prey fish community, which can be induced via size-selective fisheries, predation or shifts

in food-web configuration (Huss et al. 2012, 2014), can have various effects on the dioxin exposure to differently sized salmon (Huss, Jacobson, Gårdmark, In prep.). Thus, accounting for the size-dependency of the interaction between salmon and its prey at sea could lead to new insights regarding how hazardous substances such as dioxins are transported across trophic levels in size-structured aquatic food-chains and for evaluating management methods suggested to be suitable for decreasing hazardous substances in fish, such as increased fishing.

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Popular science summary

The species I have primarily focused on in this thesis is the Atlantic salmon (*Salmo salar*), and mainly salmon which originate from rivers connected to the Baltic Sea, known as Baltic salmon. Baltic salmon conduct a remarkable journey throughout their life. They are born in rivers in which they establish territories that they defend against other salmon. After one to several years in the river, during which the salmon have grown larger, they become silvery and start to swim with the current, with the goal to reach the sea. Once at sea, they start to feed on other fish and grow fast. Salmon stay for one to several years feeding and growing at sea until they eventually decide to swim back to their birth river to produce offspring of their own. As salmon stop feeding once they reach their home river, they rely on energy reserves stored while feeding at sea to survive the upstream migration and to successfully spawn. However, we have limited knowledge about what determines what salmon feed on at sea and how their diet affects their survival, growth, and possibilities to store energy.

In this dissertation, I have used several large datasets, statistical analyses and mathematical models to investigate whether factors that affect 1) what salmon feed on at sea and, 2) how their feeding, in turn, affects their survival, growth, and possibility to store energy is important for understanding how salmon will be affected by changes in their environment both in the river and at sea. I show that Baltic salmon mainly feed on herring, *Clupea harengus*, and sprat, *Sprattus sprattus*, at sea, and that the amount of herring and sprat they eat depends on their body size and the body size of herring and sprat, as well as where they feed at sea. I further show that the amount of energy reserves that salmon can store before they swim back to their birth river depends on the amount of consumable herring and sprat in their surroundings.

I also show that salmon feed in different regions of the Baltic Sea and that the region they feed in depends on in which river they were born and how large they are. This means that the amount of herring and sprat of the right size for salmon to feed on will not be the same for all salmon in the Baltic Sea. In

addition to these results, I found that growth at sea differed between salmon born in river Dalälven compared to salmon born in river Umeälven. This difference in growth likely occurred because salmon from these two rivers preferred to seek food in different regions of the Baltic Sea with different amounts of prey. Growth at sea also contributed to explain how much roe adult salmon produced annually in Dalälven.

I further show that salmon can be affected differently by changes in how much food there is in the river and how much salmon that are caught by fisheries, depending on if salmon compete for food at sea and how much food there is at sea. These findings can be important to consider when planning projects aiming to increase the number of salmon, such as projects aiming to improve river habitats for salmon, and when making decisions about how much salmon we should fish.

In summary, the results in this thesis show that the body size of salmon at sea greatly controls what they will eat and how much prey they have available while at sea, which in turn affects their possibilities to store energy and can cause differences in their growth. As the growth and energy reserves of individuals at sea can affect the population's development over time, these findings are important to consider to understand how salmon populations will be affected by environmental change at sea.

Populärvetenskaplig sammanfattning

Den art jag främst studerat i denna avhandling är Atlantlax (*Salmo salar*) som härstammar från älvar som mynnar ut till Östersjön, även kallad Östersjölox. Laxen gör en beaktansvärd resa genom livet. Den föds i älvar där de håller revir som de försvarar mot andra laxar. Efter att laxen spenderat ett till flera år i älven och växt sig större börjar den simma med strömmen, med siktet inställt på havet. Väl till havs livnär den sig på andra fiskar och den växer snabbt. Laxen söker föda och växer i havet under ett till flera år innan den simmar tillbaka till älven den föddes i för att producera egen avkomma. När laxen når sin ursprungsälv slutar de äta och förlitar sig istället på de energireserver den byggt upp under sin tid till havs för att orka med uppströmsvandringen samt fortplantningen.

I denna avhandling har jag använt flera stora dataset, statistiska analyser och matematiska modeller för att undersöka om vi bör ta hänsyn till faktorer som påverkar vad 1) lax åter till havs och, 2) hur laxens föda i sin tur påverkar deras tillväxt, deras möjlighet att bygga upp energireserver och överlevnad till havs för att förstå hur lax kommer att påverkas av förändringar i deras livsmiljö, både till havs och i älven. Jag visar i denna avhandling att Östersjölox huvudsakligen äter strömming, *Clupea harengus*, och skarpsill, *Sprattus sprattus*, till havs och att mängden strömming kontra skarpsill de äter beror på laxens kroppsstorlek, bytenas kroppsstorlek samt vart i Östersjön laxen befinner sig. Jag visar även att laxens förmåga att bygga upp energireserver innan de simmar tillbaka till sin ursprungsälv beror på mängden strömming och skarpsill av lämplig storlek i dess omgivning som de kan äta. Jag visar också att lax söker sin föda i olika delar av Östersjön beroende på i vilken älv de är födda och hur stora de är. Detta innebär att mängden tillgänglig strömming och skarpsill till havs kommer vara olika för olika laxar, då mängden strömming och skarpsill varierar mellan områden i Östersjön.

Utöver dessa resultat så visar jag även att laxens tillväxt till havs skiljer sig mellan lax född i Dalälven och i Umeälven. Att lax från dessa två älvar växer olika till havs beror sannolikt på att de föredrar att söka sin föda i olika delar i

Östersjön, vilka variera i mängden tillgängliga byten vilket i sin tur styr laxens förmåga att växa. Tillväxt till havs bidrog även till att förklara mängden rom som adulter producerat årligen i Dalälven.

Slutligen så visar jag att beroende på om lax konkurrerar om mat med varandra i havet eller inte så kommer de sannolikt att svara olika på förändringar i mängden mat de har i sin älv samt på hur mycket vi fiskar. Dessa resultat visar på att vad lax äter till havs, samt om de konkurrerar om maten med andra, är viktigt att ta hänsyn till när man planerar projekt som syftar till att öka mängden lax, såsom habitatförbättrande åtgärder i laxens ursprungsalv samt för beslut gällande hur mycket lax vi fiskar.

Sammanfattningsvis visar resultaten i denna avhandling att laxens kroppsstorlek styr vad den kommer att äta och hur mycket byte den har att tillgå till havs, vilket i sin tur påverkar deras förmåga att lagra energi och kan orsaka skillnader i tillväxt till havs mellan lax födda i olika älvar. Eftersom individers tillväxt och förmåga att lagra energi kan påverka hur populationer utvecklas över tid, är dessa resultat viktiga att ta hänsyn till för att förstå hur lax kommer att påverkas av miljöförändringar både i dess älv, till havs samt vid ett förändrat fiske.

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The body size and feeding of individuals largely determine their survival, growth, and reproduction success, which in turn affect the dynamics of populations. In this thesis, I show that accounting for individual food- and size-dependent processes, in combination with size-dependent predator-prey interactions of salmon at sea is important for understanding their population dynamics and how salmon and other anadromous fish species will respond to environmental change and changes in fisheries.

Philip Jacobson received his graduate and undergraduate education at Stockholm University.

Acta Universitatis Agriculturae Sueciae presents doctoral theses from the Swedish University of Agricultural Sciences (SLU).

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