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Scales of density dependence: Implications for Baltic salmon (*Salmo salar*) and sea trout (*Salmo trutta*) stock assessment

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Front cover:
Salmon eggs from the Fisheries Research Station, Älvkarleby, used in competition experiments.
Photo: Stefan Skoglund, SLU.

Back cover:
Bowery Creek, New York. Photo: Stefan Skoglund, SLU.

Abstract

Density dependence is a fundamental concept in fisheries ecology and underpins most of the dynamic patterns observed in fish populations. Moreover, compensatory density dependence allows sustainable harvest of natural populations, where a reduction in numbers (through harvest) is offset by an increased rate of population growth. Fisheries stock assessments capture density-dependent survival in the early-life or juvenile stage through a stock-recruitment relationship, however, a rising number of studies suggests that density-dependent processes also might act during later life stages. Moreover, stock-recruitment models often assume that density-dependence occur at the population level, such that all individuals in a given life stage would interact with each other. In reality however, density-dependence may act primarily over small spatial, and temporal scales, and where inter-cohort competition generates additional complexity to the process. Omitting density dependent processes from assessment models, or ignoring the scale at which they act could lead to bias in estimates of stock-status and productivity, potentially undermining sustainable fisheries management. Baltic salmon and sea trout, two commercially and recreationally important fish species, spawn in freshwater riverine systems characterized by heterogeneously distributed habitats which generate locally and temporally high densities of juveniles. Combined with low dispersal abilities, fine-scale density-dependent factors are potentially more prone to shape the population dynamics which might not only affect survival but also the maturation rate. In this introductory essay I explore the concept of density dependence in general, and how available knowledge is or might be used in fisheries management and stock assessment models, in order to make unbiased estimates of natural fish population, with a focus on the Baltic Sea salmon (*Salmo salar*) and sea trout (*Salmo trutta*). Even though density-dependent processes for the two species has been extensively studied, and incorporated in stock assessment models, there are still some knowledge gaps to fill (e.g. interspecific competition in the earliest life stage), that might improve the models. I will evaluate how we can use additional information of density-dependent processes for salmon and sea trout, based on existing data and new knowledge gained from experimental work, to potentially obtain more unbiased parameter estimates in the stock assessment models, in order to improve the potential for sustainable harvest of natural resources.

Keywords: Density dependence, spatial scale, salmon, sea trout, stock assessment, fisheries ecology.

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Abbreviations

DD	Density Dependence
DI	Density Independence
ICES	International Council for the Exploration of the Sea.
IDD	Inverse Density Dependence
MSY	Maximum Sustainable Yield
WGBAST	Baltic Salmon and Trout Assessment Working Group

1 Introduction

Groups of individuals of the same species, sharing the same defined area of sufficient size (populations) are not static in their abundance. The dynamic pattern of population abundance is regulated via density-independent and density-dependent factors, sometimes also denoted as exogenous and endogenous factors, respectively (Cherrett & Bradshaw 1989; Murdoch 1994; Sinclair & Pech 1996; Turchin 1999). Density-independent factors are those that affect population growth but are not themselves affected by the number of individuals in a population (e.g. the environment), whereas density-dependent factors generates both positive (e.g. the Allee effect), and negative (e.g. compensation) feedback mechanisms influenced by the number of individuals in a population (Sinclair, 1989; Royama, 1992; Turchin, 1999). The concept of density dependence is that a change in abundance will lead to a change in demographic rate, e.g. increasing number of individuals will generate a higher mortality rate due to increasing competition among individuals (Nicholson 1933; Sinclair 1989; Turchin 2003). This regulatory mechanism reduces unbounded fluctuations of the population abundance and impedes extinction (Nicholson 1933; Murdoch 1994; Sinclair & Pech 1996). Density dependence is a fundamental concept in ecology and relates to most phenomena observed in nature, it is crucial to understand in order to make accurate predictions of population fluctuations, and further, to succeed with management and conservation efforts (Royama 1992; Murdoch 1994; Sinclair & Pech 1996; Turchin 1999, 2001, 2003).

In fisheries ecology and fisheries management, density-dependent regulation is a central concept, since compensatory density dependence is the mechanism that allows sustainable harvest of natural populations (Haddon 2001; Pauly *et al.* 2002; Walters & Martell 2004; Herrando-Pérez *et al.* 2012; Eikeset *et al.* 2016). For commercially important fish populations (stocks), density-dependent regulatory factors have been well studied and detected (Rose *et al.* 2001), where the main driving density-dependent factor is suggested to be intraspecific competition for food (Beverton & Holt 1957; Elliott 1994; Haddon 2001; Lorenzen & Enberg 2002). However, depending on what scale that density dependence is studied, the effect might be imposed through other mechanisms than competition for food, e.g. predation (Hixon & Carr 1997) or diseases (Krkošek 2017). Density-dependent regulation in fish populations might also act differently depending on the demographic scale, where populations could be affected both through direct effects, e.g. juvenile or adult mortality rates (Imre *et al.* 2005; Lorenzen & Enberg 2002; Lorenzen 2008), and/or via indirect effects such as decreased in individual growth rate (Amundsen *et al.* 2007), possibly leading to delayed maturation and decreased fecundity (Wootton 1998). Density-dependent mechanisms in fishes are most pronounced in the juvenile stage (Sinclair 1989), but have also been detected in the adult stage for some fish species (Lorenzen 2008; Andersen *et al.* 2017).

To date, most studies on the mechanisms and consequences of density dependence do not consider the spatial scale at which it acts (e.g. Beverton & Holt 1957; Ricker 1975). In nature, resources are heterogeneously distributed and mobile organisms are assumed to redistribute themselves in response to this spatial variation of resources, in order to obtain maximum fitness (Fretwell & Lucas 1969). It is often assumed therefore, that in continuous habitats (e.g. rivers), local density dependence might not be present. However, when for example adult preference of breeding habitat is pronounced, high densities of juveniles could induce density-dependent effects on local scales (Einum & Nislow 2005; Einum *et al.* 2011b). This local, or even fine spatial scale dynamics of density dependence is something that needs further studies in order to obtain higher predictive power of population models (Einum & Nislow 2005; Rogers *et al.* 2017).

Anadromous fish species (e.g. Salmonids) are highly studied with respect to density dependence, however, only a small proportion of the literature has focused on the importance of local dynamics (Einum & Nislow 2005; Finstad *et al.* 2009; Einum *et al.* 2011b, a). Most studies demonstrate strong patterns of density-dependent mortality during the juvenile life phase, and for migratory salmonids this pre-recruit life stage is mostly restricted to fluvial freshwater habitats (Verspoor *et al.* 2007). Since these nursery habitats have spatial delimitations, territorial behaviour in juvenile salmonids might force intra- and inter-cohort competition for resources leading to density-dependent mortality or decreased body growth rate (Kalleberg 1958; Cutts *et al.* 1999; Einum *et al.* 2006, 2011b; Vincenzi *et al.* 2012; Höjesjö *et al.* 2015).

The Atlantic salmon (*Salmo salar*) and anadromous brown trout (“sea trout”; *Salmo trutta*) are important anadromous salmonids, not only for generating high economic incomes from recreational and food exploitation, but they are also keystone top-predatory species in many waters (ICES, 2017). Due to their high value many native salmonid populations suffer from over-exploitation, and together with the loss or degradation of life-history vital habitats, many natural populations today are considered endangered or even extinct (Limburg & Waldman 2009). Population dynamics of the Atlantic salmon has been well studied (Wańkowski & Thorpe 1979; Klemetsen *et al.* 2003; Einum *et al.* 2006; Verspoor *et al.* 2007; Aas *et al.* 2010; Einum *et al.* 2011b; Höjesjö *et al.* 2015; Wolter 2015), whereas mechanisms shaping variation in sea trout abundance is not fully understood (Elliott 1994; Degerman *et al.* 2012). This might be due to the more complex life-history characteristics of the sea trout compared to salmon (see section 4.2 for more details). Moreover, the potentially interspecific competition affecting density-dependent responses in rivers where the two species co-exist is still understudied. Territorial behaviour and habitat preference for the two species has been well studied, showing a difference in in-river habitat occupation (Kalleberg 1958; Jones 1975). However, most of these studies look at the competition between the two species at a relatively late juvenile phase (1month-1+ year), and the potential intra- and interspecific density induced competition in the earliest stage, directly after emergence, is still not studied. This is a phase of the lifecycle where the two species potentially occupy the same habitat and initially at high densities. This mechanism is probably most occurring over a fine spatial scale.

Density-dependent processes are important population regulatory mechanisms incorporated in fisheries management, however many stock-recruitment models use population overall density-dependent factors whereas the effect might be most pronounced at a fine scale, both spatially (Einum & Nislow 2005) and demographically (Dingsør *et al.* 2007; Andersen *et al.* 2017). In my doctoral thesis the aim is to evaluate the importance of local population dynamics for salmon and sea trout, trying to identify at what scale density-dependent mechanisms acts. This in order to improve existing population models including density dependence and thereby potentially strengthen conservation and assessment efforts for these two commercially important fish species. This will be done by: 1) Evaluate how the incorporation of fine-scale density-dependent processes might improve a two parameter stock-recruitment model, comparing models assuming "whole-system" density dependence, versus models including local scale density dependence. 2) Evaluate if small scale density-dependent processes could be derived from existing collative data from salmon and sea trout samplings (e.g. smolt and spawner counts, habitat quality etc.) or if other national sampling methods are needed to detect population dynamics on a fine scale. 3) Investigate the potential process of interspecific competition between salmon and sea trout, and more specific the influence of density-dependent competition on a small spatial scale in the earliest life-stage. 4) Study the potential improvement in using additional data in the parr to smolt estimates, incorporate factors important in this process (e.g. temperature, habitat characteristics and parr length). 5) Combining the results from the above stated research points, in order to evaluate how today’s used population models for salmon and sea trout might be alternated to potentially improve the predictive power of existing models.

In this essay, I review the literature in the field of density dependence, with a focus on fish in general and salmon and sea trout in particular, in order to obtain a solid theoretical background in the research field, and moreover, identify potential knowledge gaps where my doctoral work might contribute to the understanding of density-dependent mechanisms, influencing ecological process observed in nature.

2 Population regulation

As early as 1798, T. R. Malthus suggested that a population will grow geometrically until it reaches its limits of available resources. Following this concept, the size of a population cannot increase to infinity. A Population that is regulated most show three related characteristics: 1) Persistence, where a population will survive for many generations without exhibiting random-walk patterns, 2) boundedness, where the fluctuations of the population density remains in between some upper and non-zero limits and 3) return tendency, where a population will decrease in abundance above a certain size (carrying capacity) and increase when abundances are below a certain size (Murdoch 1994; Turchin 2003; Hixon *et al.* 2012). Even if regulation could be induced by density-independent factors (e.g. predation or harvest) on some demographic or temporal scale, a density-dependent response mechanisms on at least one demographic rate is essential for long-term population persistence (Sinclair 1989; Murdoch 1994; Turchin 2003). This concept is today accepted, but has historically caused debates among ecologists.

2.1 Historical background

In the last six decades there has been arguments amongst ecologists concerning the actual existence of density dependence and population regulatory mechanisms (Andrewartha & Birch 1954; Andrewartha 1957; Milne 1962; Reddingius & den Boer 1970; Sinclair & Pech 1996; Murray 1999; Turchin 1999; Berryman 2004; White 2004). The two camps of debaters regarding population regulation and density dependence, mainly constituted by Andrewartha and Birch (1954) and Nicholson (1954), and both parts were partly correct in their arguments. Nicholson was correct in that regulation needs to be induced by density-dependent factors, however, competition is not the solely mechanism driving it. Other factors like predation and disease might also be density-dependent (Sinclair & Pech 1996; Turchin 2003). Andrewartha and Birch, on the other hand, were correct about that the density-independent factors in the environment could induce predation or affect limiting factors that generates fluctuation of populations. However, density-independent factors alone cannot explain the long-term regulation of populations, since populations at low densities via compensatory mechanisms can survive over long periods without going extinct (Turchin 1999; Hixon *et al.* 2002; Rose *et al.* 2001). Today the majority of ecologists do not argue anymore whether or not all populations are regulated by density-dependent factors. Instead the general agreement is that both density-independent and density-dependent factors affects populations, but that their relative regulatory strength might vary between different populations and environmental conditions (Turchin 1999).

2.2 Logistic growth

The most basic conceptual model containing a regulatory expression, is the logistic model of growth (Verhulst 1838). The concept of the logistic growth model is that an undisturbed population, if persisting, will increase in abundance and eventually reach some point of equilibrium where density dependent mechanisms will cause oscillation in abundance around the equilibrium point (Nicholson 1933; Cherrett & Bradshaw 1989; Murdoch 1994). This equilibrium is generally the carrying capacity (K) of a system at a given time, where limiting factors (e.g. resources) controls the maximum abundance (N) of a population (Turchin 2003). When N increase over time (t) and approaches K, the growth rate should slow down and become 0 when N=K. This part is incorporated in the logistic growth model

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right), \tag{1.}$$

where the per capita population change over discrete time steps, *dN/dt*, will be restrained by the self-regulatory mechanism represented by (1-*N*/*K*). *r* is the intrinsic growth rate which is the per capita change of individuals per reproducing individual. For logistic growth over continuous time, the equation is given as:

$$N_t = \frac{N_0 e^{rt}}{1+N_0(e^{rt}-1)/K}. \tag{2.}$$

The concept of the logistic growth model is that the increase in abundance is slow when population abundance is low, due to the low number of potential reproducing individuals that contribute to the next generation. When the population approaches carrying capacity, limiting factors decrease the population growth rate, and at N=K the population abundance is constant over time (Fig. 1). The growth rate is highest at the steepest point of the curve (approximately K/2).

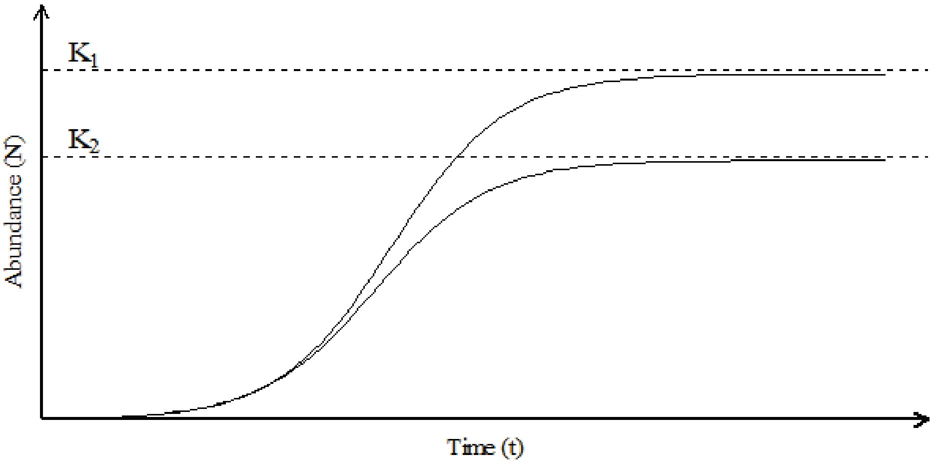

Figure 1. Illustration of logistic growth in two populations with same N0 and r (equation 2) but different carrying capacity (K1 and K2). The abundance increases exponentially over time until it levels off. Depending on K (here illustrated by dashed lines) the potential maximum abundance of a population will be different, where K1 can sustain more individuals compared with K2.

In nature, however, it is uncommon to observe static population abundance exactly at equilibrium, since environmental (e.g. natural and anthropogenic perturbations) and demographic (e.g. random births, deaths and sex ratios) stochasticity will induce fluctuations in the population abundance, (Rose *et al.* 2001; Hixon *et al.* 2002). Therefore, natural populations at N = K, will not have a static abundance, but more likely fluctuate around K where the amplitude of the fluctuations will be influenced by the strength of density-dependent mechanisms and the response from environmental perturbations (Sinclair & Pech 1996; Haddon 2001; Hixon *et al.* 2002). Although belonging to basic ecology concepts, the logistic growth model captures the important aspects of density-dependent population growth and makes out the foundation for many population models, and is therefore a good way to introduce and exemplify density dependence.

2.3 Density dependence

If a population is regulated, at least one demographic rate (e.g. per capita birth rates and/or death rates) must be density-dependent (Turchin 2003; Hixon *et al.* 2012)(Fig. 2a-c). Density-dependent processes affects individuals of a population in various ways, e.g. habitat selection (Teichert *et al.* 2017), movement (Einum & Nislow 2005) and/or individual body growth (Einum *et al.* 2011b), and the driving forces are competition, predation and diseases (Murdoch 1994; Sinclair & Pech

1996; Hixon *et al.* 2002). Competition for a limiting resource is per definition always density-dependent, either via interference (direct interaction) or exploitation (indirect interaction), and the specific response could both affect the input (e.g. fecundity) or the output (e.g. mortality) for the individual, which induce a response on a population level (Rose *et al.* 2001; Hixon *et al.* 2002). Predation on the other hand is not always density-dependent. To act as regulatory, the predator total response (the product of functional and numeric response) has to increase the per capita mortality rate of the prey with increasing prey densities (Sinclair & Pech 1996). Predation might also interact with competition induced by density-independent factors. In a long-term field experiment, made by Hixon *et al.* (2012), an environmental factor (abundance and distribution of spatial refuges) induced a density-dependent mortality, where predation acted as the mortality agent. This illustrates the complexity of density-dependent processes and the importance of including different types of density-dependent mechanisms and processes when studying density dependence. The vast variety of density-dependent processes has been thoroughly reviewed and compiled by (Herrando-Pérez *et al.* 2012), and I will in this essay only explain the processes most relevant to my doctoral thesis.

2.3.1 Compensatory density dependence or compensation

Compensatory density dependence (hereafter termed compensation) is when rates (e.g. growth, survival, reproduction and movement) change in response to variation in the population density so that the population numerical growth rate will decrease at high densities and increase at low densities (Rose *et al.* 2001). Density-dependent mortality and reproduction rates directly affect the number of individuals, whereas other density-dependent processes, e.g. fecundity (Cresswell *et al.* 1992; Ferrer & Donazar 1996; Ferrer *et al.* 2006), individual body growth (Myrvold & Kennedy 2015), predation (Hixon & Jones 2005; Dingsør *et al.* 2007) and/or dispersal (Einum *et al.* 2011b), are not regarded as compensatory if they do not ultimately affect the population abundance (Rose *et al.* 2001). For example, a decrease in individual body growth that does not affect mortality or reproduction will only generate smaller individuals and will not affect the population density, even if the initial cause is due to density dependence. Thus, no compensation has occurred. The strength of compensation could be defined as the rate of change in a demographic parameter as a response of change in population densities, e.g. represented by the slope of a population growth model, where a larger first derivate reflects stronger density-dependent effects and vice versa (Sinclair & Pech 1996). However, this strength might differ between populations and is dependent on the population model. Compensation is the mechanism that allows sustainable exploitation of many natural populations, where a reduction in numbers (through harvest) will ease a compensatory mortality, and where increase in fitness among the remaining individuals will contribute to a more productive state of the population (Sinclair & Pech 1996; Walters & Martell 2004). In particular, the concept of compensatory mechanisms is central to fisheries ecology and fisheries management (Myers *et al.* 1995; Myers 2001; Rose *et al.* 2001).

The strength of the compensatory response can shape the temporal dynamics in the abundance of unharvested populations. In stable systems where compensatory effects are weak, stochasticity in the population fluctuation is mainly caused by density independent factors (Sinclair & Pech 1996). When it takes just one time step for a population to rebound to its equilibrium, after a perturbation event (e.g. a change in the environment or altered predation), it is said to exhibit perfect or exact compensation, whereas if it takes more than one time step to rebound the population is said to be regulated by undercompensation (Turchin 2003). These two relatively weak compensatory response patterns will generate more “stable” dynamics in the abundance. Populations that display large fluctuations or cyclic oscillation patterns in abundance over time, are said to overcompensate (Sinclair & Pech 1996; Turchin 2003). Overcompensation is most common in populations with strong hierarchical or size variated population structures, where for example removal or harvest of large individuals can generate a rapid increase of smaller individuals (Zipkin *et al.* 2008). Such a feed-back pattern might also induce density-dependent population crashes (Sinclair & Pech 1996). In Soay sheep (*Ovis aries*) populations, for example, the dynamics seems to be altering between periods with or without overcompensation, and this pattern is highly influenced by environmental dynamics (Coulson *et al.* 2001). This indicates that compensation is not a mechanism that is static over time, and that the compensatory patterns might be influenced by changes in the environment.

2.3.2 Inverse or depensatory density dependence

Depensatory density dependence, is the reverse of compensatory density dependence, where the mortality rate decreases with increasing population density and vice versa (Fig. 2a). Depensatory density dependence is commonly seen for predation, where for example larger groups of predators might increase individual hunting success generating an increase in survival, compared to solitary food search (Major 1978). However, if prey becomes scarce or if the predator population exceeds carrying capacity, intraspecific competition for food might decrease survival rates. The Allee effect is a form of depensatory density dependence, where reproduction deficiencies at low population densities may induce a negative population growth, even at densities where density-dependent mortality rates are almost zero (Allee 1941;

Courchamp *et al.* 1999). Detection of depensation is especially important in depleted populations, since it may accelerate further decline of the population, and potentially delay recovery or even result in extinction (Shelton & Healey 1999). Depensation could be present at both high and low abundances but has been hard to detect in many populations. One of the main reasons for that is the absence of data at extreme population densities (both high and low). (Perälä & Kuparinen 2017) illustrate the effect when the extreme density observations are absent. By using observation data from Atlantic herring (*Clupea harengus*) and sequentially removing low spawning stock observations, the stock-recruitment model (see section 3 for detailed information on stock-recruitment models) eventually fails to detect the depensatory process in the population. Absence of data at extreme population densities are relatively common in time-series, and percussions needs to be taken when extrapolating this type of data. Beverton and Holt (1958) suggest that when data do not cover low population densities, a sigmoidal growth model (Schaefer 1954) should be used, in order to capture potential depensatory population dynamics.

2.3.3 Delayed density dependence

In some cases, both compensatory and depensatory density dependence processes could be delayed, making them more difficult to detect. Delayed density dependence could be detected from time-series analysis, where the mortality rate is affected by earlier events in the population density and where there are time delays in the density dependence. Delayed density dependence will create an anti-clockwise pattern for mortality rate if plotted against population density following each time step (Sinclair & Pech 1996) (Fig. 2d). This type of regulation may for example be observed where predators has delayed response to increasing prey abundance, which can cause large oscillations in the abundance for both the predator and prey population, as observed for winter predation of lynx (*Lynx canadensis*) on snowshoe hare (*Lepus americanus)* (Trostel *et al.* 1987). It is also commonly observed in parasite and host dynamics (Burthe *et al.* 2006).

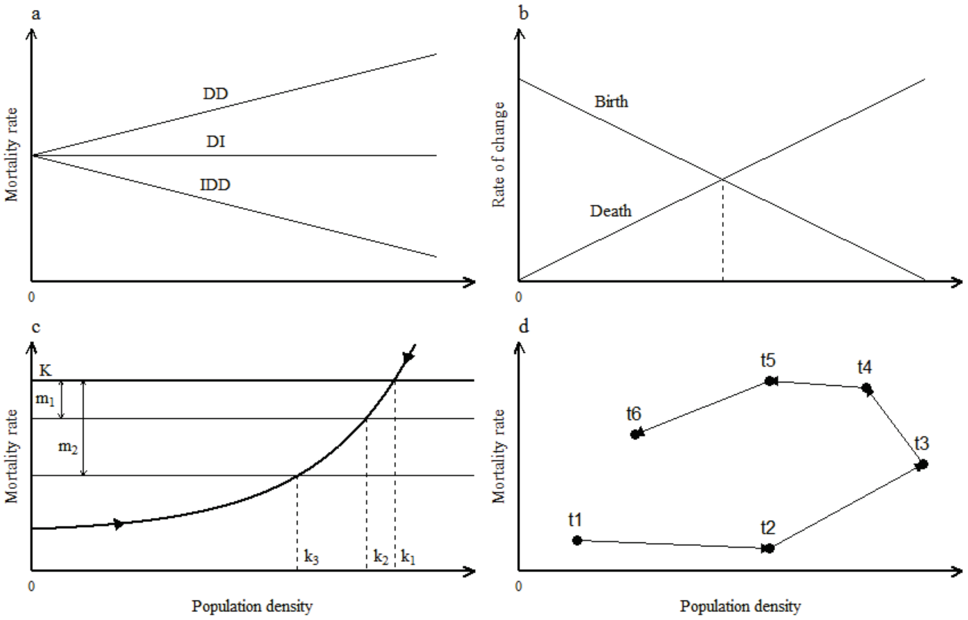

Figure 2a-d. Conceptual descriptions modified after Sinclair and Pech (1996) and Hixon et al. (2002), illustrating density dependence (DD) in relation to density independence (DI) and inverse density dependence (IDD). (a) Response in mortality rate if populations excites DD, DI or inverse IDD. (b) Compensatory response in demographic rate of change, here illustrated by the per capita change of births and death over time at different population densities. Where the two lines cross (dashed line) the change in population abundance is zero. (c) Mortality rate illustrated for a more realistic case (than in a) of density dependence (DD) using an exponential curve. In this case (c) the production is hold constant and at the maximum production (K) the first equilibrium point is reached (k1), in nature the production is equivalent with the carrying capacity. Inducing additional density-independent mortality (m1 and m2) the equilibrium point will shift to lower population densities (k2 and k3; i.e. yielding a lower level of carrying capacity). (d) Illustration of delayed density dependence, where mortality rate over time first shows an inversed density dependence with growing population but via e.g. increasing predator response, the mortality rate will increase and eventually decrease as population densities decrease.

3 Fisheries ecology and stock assessment

Fisheries ecology is the field of science where the main aim is to describe the population dynamics of fish species that are targeted by fisheries. Population models based on concepts from theoretical ecology are used to obtain estimates of the status (e.g. abundance, fishing mortality etc.) and development of exploited populations (Quinn & Deriso 1999). For practical reasons, several local populations are often pooled to represent a stock of a targeted fish species. Such a pooled stock most likely comprises populations that experience different local habitat characteristics, and thus the strengths of density-dependent and –independent factors might differ. Therefore data from both large spatial and temporal scales are important for stock assessment (Kareiva *et al.* 1990; Hixon *et al.* 2012).

Since exploited fish stocks experience multiple life-history stages, and owing to the fact that density-dependent and –independent factors act differently at different life stages, our understanding of the scale and relative effects of these factors must be incorporated in stock-assessment and fisheries ecology (Myers 1995; Turchin 1999). The life-cycles of fishes are often divided into the pre-recruit phase, from hatching to the late or advanced juvenile individual, and the recruited phase that includes the maturation phase to spawning. The latter phase is typically the part of the life-cycle where harvest of fish populations occur (Russell 1931; Lorenzen 2008; Rose *et al.* 2001). In the pre-recruit phase it is mainly competition for resources that generates density-dependent mortality (Elliott 1994), while in the recruited phase the mechanism is mainly intra- and interspecific competition, leading to reduction in body growth and potentially decrease in fecundity (Lorenzen & Enberg 2002; Lorenzen 2008).

Age-structured models are most widely used in stock assessment (Walters & Martell 2004), but there are many types of stock assessment models that differs in objectives, complexity, parameters and data requirements.

3.1 Surplus production models

Sustainable harvest is an over-arching goal of fisheries management aiming to harvest only the surplus of a fish stock (Haddon 2001; Walters & Martell 2004). Surplus-production, is the production of a fish stock over and above that needed to replace the loss of individuals due to natural mortality (Haddon 2001). Surplus production models or Schaefer models (Schaefer 1954), also known as biomass dynamic models or stock production models, are population models that aggregate data across age classes. These models are used to search for the highest fishing mortality that can be offset by increased population growth, where the yield is most commonly measured as biomass change over several time steps (Jennings *et al.* 2001). This maximum production rate or yield is termed the Maximum Sustainable Yield (MSY) (Schaefer 1954; Haddon 2001; Walters & Martell 2004). Where the aim is to harvest a proportion of a targeted fish stock leaving enough recruits to sustain a viable population (a population that does not decrease in numbers). If we instead use the differential equation of the logistic growth rate equation (equation 1), and view it graphically (Fig. 3), we obtain the maximum reproductive rate where the slope of the first derivate is zero. This point is equal to the MSY. The MSY is a very narrow goal, and moreover a moving target. Precaution suggests that management should aim for yields below the MSY in order not to risk overexploitation and stock collapses (Jennings *et al.* 2001).

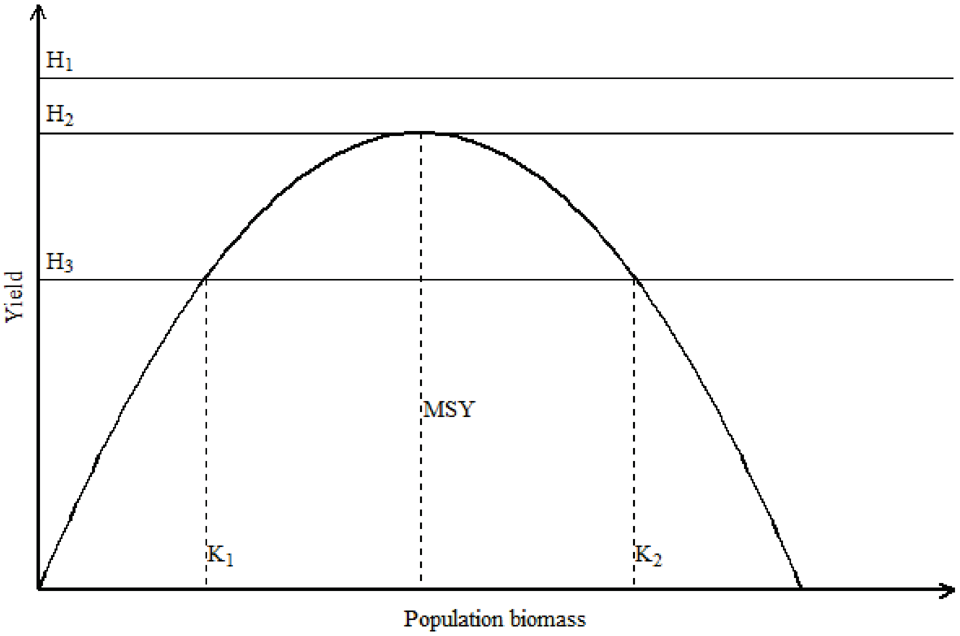

Figure 3. Illustration of the yield over increasing population size. The maximum sustainable yield (MSY) is obtained when the production rate reaches maximum. Depending on the harvest that is practiced (three alternatives shown; H1-H3) the population could reach different equilibrium states (K1, K2 and MSY). At H2 the equilibrium point is SMSY, the population biomass at which the maximum harvest can be taken without reducing the population size. Higher harvest rates (e.g. H1), will overharvest the stock and reduce the population size over time. If the proportional harvest is lower than HMSY (e.g. H3), two equilibriums could be possible, e.g. K1 or K2, depending on the initial population size when the harvest is introduced. If the spawning stock size is below K1 (under harvest-scenario H3) the population will grow until it reaches equilibrium at K1, if it is between K1 and K2, it will grow until it reaches equilibrium at K2.If the population is above K2 when fishing is introduced, the population will decrease until it reaches the equilibrium point K2.

3.2 Virtual population analysis (VPA)

These analysis uses fisheries data to calculate the stock size and mortality rates of age- or length-based cohorts. The concept of VPAs is to rebuild the historical stock size by adding fisheries and natural mortality, and from that estimate the initial stock size of a certain cohort (Quinn & Deriso 1999; Haddon 2001; Jennings *et al.* 2001; Walters & Martell 2004). VPA is not a statistical analysis, but is used extensively in fisheries ecology, and for heavily exploited fish stocks, to provide a good estimate of the recruitment, which is hard to observe for many marine fish stocks. When first introduced by Gulland (1966) it was used for single species stock assessment, today it is widely used in multispecies stock assessment.

3.3 Statistical catch at age models

In age-structured models, the status of a fish stock is usually estimated from the relationship between stock size and recruitment. The optimal measurement of a spawning stock is the eggs spawned during spawning seasons (Rothschild & Fogarty 1989; Kell *et al.* 2016), and in most stock-recruitment models the biomass (or numbers) of the spawning proportion of the population is frequently used as a proxy for egg production or reproductive potential, whereas recruitment is measured as the number or biomass of individuals returning to the stock after a defined time or age, normally at the age that the individual will be detectable (either by fisheries or surveys)(Ricker 1954, 1975; Beverton & Holt 1957; Lorenzen 2008; Kell *et al.* 2016). Reproductive capability is typically hard to measure directly but may be estimated indirectly from average fecundity per age-class and the proportion of each age-class in the stock, or alternatively from the number of mature females multiplied by the average fecundity or the biomass of mature individuals (Haddon 2001). For some freshwater species the number of recruits may be counted via different methods (e.g. fish counting machines in rivers), but for most exploited fish stocks it is only possible to estimate relative abundance (e.g. from trawling and fish survey data).

The stock-recruitment relationship is used in most of the standard "dynamic-pool" fisheries models (Beverton & Holt 1957; Ricker 1975), and assumes that the density-dependent mortality occurs exclusively in the juvenile phase (Lorenzen 2008). However, Lorenzen (2008) showed that for some populations density-dependent growth regulation was stronger in the mature phase, and that this regulation might be most important when populations are close to carrying capacity. Hence, identifying the life-history stage where potential density-dependent factors may act is of great importance in population ecology and stock assessment, and the majority of the density dependent mortality might act on fine demographic and temporal scales.

There are several mathematical descriptions of stock-recruitment relationships, but in this essay I will focus on the Beverton-Holt (Beverton & Holt 1957), and the Ricker (Ricker 1954) stock-recruitment models, the two most widely-used in fisheries science, also the most commonly used for salmonid fish.

3.3.1 Beverton-Holt model

Beverton and Holt (1957) studied data on spawning stock biomass and number of recruits in fish species. They noted that spawning stock biomass is a poor predictor of recruitment, except at very low stock densities. This fact made them realize that there must be strong density dependent mortality acting at the juvenile life stage, that juvenile survival decreased with increasing spawning stock density, and that this density-dependent mortality was likely induced by intra-cohort competition in the juvenile life stages. From these observations and deductions they derived the Beverton-Holt spawning stock-recruitment equation:

$$R = \frac{\alpha S}{1+\alpha\frac{S}{K}}. \qquad (3.)$$

This is just one of many versions of the Beverton-Holt spawner stock-recruitment function. R represents recruits and S is the spawning stock. α is the maximum survival of recruits, or the density independent factor (the slope of the model when S is close to zero); this density-independent mortality represents the product of all density-independent mortalities connected to the different life stages and juvenile life-history shifts. K is the carrying capacity, and captures the density-dependent aspects of the model and generating the asymptotic shape of the curve at high spawning densities (Fig. 4). This asymptotic Beverton-Holt stock-recruitment pattern has been observed for a great number of fish species (Walters & Martell 2004).

3.3.2 Ricker model

Ricker was inspired by Nicholson (1933), to believe that the abundance of an organism has to be limited by a compensatory mechanism, and question increasing production proportional to the stock size (as the assumption was during that period). From this, Ricker (1954) suggested a model that could describe a large proportion of observed recruitment curves. The Ricker model:

$$R = \alpha S e^{-KS}, \qquad (4.)$$

suggests that the spawner stock-recruitment relationship has a dome-shaped character (Fig. 4) where the maximum recruits per spawner occurs at a medium spawner density levels. As in the Beverton-Holt equation (3), α is the density-independent parameter and K the carrying capacity. The biological mechanisms for the special phenomenon described by the Ricker function (i.e. number of recruits per capita declines again at higher spawning stock density) could be e.g. high intraspecific competition, cannibalism (Ricker 1975), spawning disturbance by other spawners (Haddon 2001) or disease outbreaks at high population densities (Krkošek 2017).

The level of MSY can be derived from stock-recruitment functions where the curve is compared with a replacement line (i.e. the line where the recruits replace the stock spawning stock size exactly), where the maximum distance between the stock-recruitment curve and the replacement line corresponds to MSY (Fig. 4). The concept of MSY is widely used as a fisheries management tool. However, for some fish stocks where there are uncertainties regarding the population size and the production capacity, a precautionary approach (Garcia 1995) is often applied; there the harvest should follow a moderate and adaptive approach where it is initially set low, but where follow up of the stock size could change the management. One more aspect is fisheries management at low densities where underlying depensatory effects might impede the recovery of fish stocks. Therefore, Beverton & Holt (1954) suggested that a sigmodal stock-recruitment function, capturing such a potential depensatory mechanism, should be applied whenever there are high uncertainties regarding relationships at low stock densities.

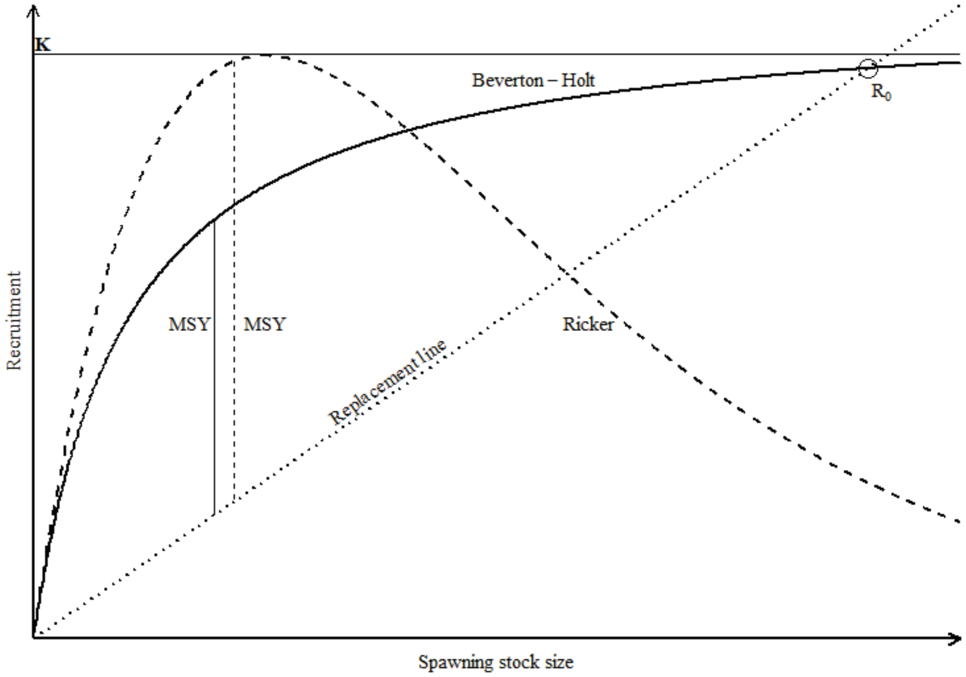

Figure 4. Illustration of the Beverton-Holt and Ricker stock-recruitment equations. The dashed line illustrates the replacement line that is equal to the exact replacement of juveniles to the spawning stock where the slope is equal to 1/eggs per recruit. The area under the stock-recruitment on the left side of the replacement line is the surplus production of the stock. Maximum sustainable yield (MSY) for the Beverton-Holt function and Ricker function is illustrated with vertical dashed lines at the point with largest distance between the replacement line and the respective curve. R0 is, for the Beverton-Holt model, the recruitment at unfished demographic equilibrium.

3.4 Summary stock assessment

As described above, density-dependent mechanisms are expected to allow sustainable exploitation of natural fish stocks. However, this involves a great deal of responsibility and knowledge about both the density-dependent and –independent mechanism that affect the population dynamics at various spatial, demographic and temporal scales. Thus, all additional information regarding the scale and strength of these effects are needed to obtain vital knowledge in the aim to use natural resources in a sustainable way. Density-dependent mortality could directly lead to compensation, but from field data it is typically hard to detect and quantify such effects, e.g. due to measurement errors, absence of long-term monitoring data or that available data do not cover the potential extreme densities of a population (Rose *et al.* 2001). However, new methods for data analysis have improved the possibility to detect and quantify density dependence (Myers 2001; Pope *et al.* 2006). Moreover, it is also important to synthesize information of a particular fish population from many sources of data (e.g. experiments, field data, simulation models) to obtain an accurate understanding of its dynamic patterns (Rose *et al.* 2001).

4 Atlantic salmon and sea trout

This section will cover the ecology of Atlantic salmon and sea trout, and the fisheries associated with these species. These two species will be the study organisms in my thesis work, evaluating the scales of density dependence in a river environment.

4.1 Atlantic salmon

The Atlantic salmon (*Salmo salar*) has been exploited throughout human history. For example, 10 000-years old cave paintings of salmon in Scandinavia suggest that salmon has been an important contributor to food security for humans throughout the development of modern human populations (Aas *et al.* 2010). An active management of Atlantic salmon is necessary for several reasons; the species generates high commercial (Mawle & Peirson 2009) and recreational values (Birkel *et al.* 2014), and is widely geographically distributed, covering both fresh and salt water habitats (Verspoor *et al.* 2007; Aas *et al.* 2010) where each river stock often crosses several national borders (Wańkowski & Thorpe 1979; Holm *et al.* 2000). Further, many salmon populations have declined in abundance during the past 30 years (Wolter 2015). As mentioned above, a stock (in fisheries management) often consists of pooled populations. Since the salmon has a complex life-history, with stages in both fresh and saltwater, the importance of understanding the dynamics of each individual population over several life-history shifts is crucial for succeeding in conservation and fisheries management efforts.

4.1.1 Biology

The Atlantic salmon is a native species in temperate and subarctic regions, and as with many other salmonids, it has a complex and diverse life-cycle (Aas *et al.* 2010). The species is anadromous, meaning that it is born in freshwater and later migrates to saltwater to mature into the spawning stage, after which it returns to freshwater to spawn. During this life-cycle the salmon undergo several morphological changes and adaptations to survive in both fresh- and saltwater (Fig. 5).

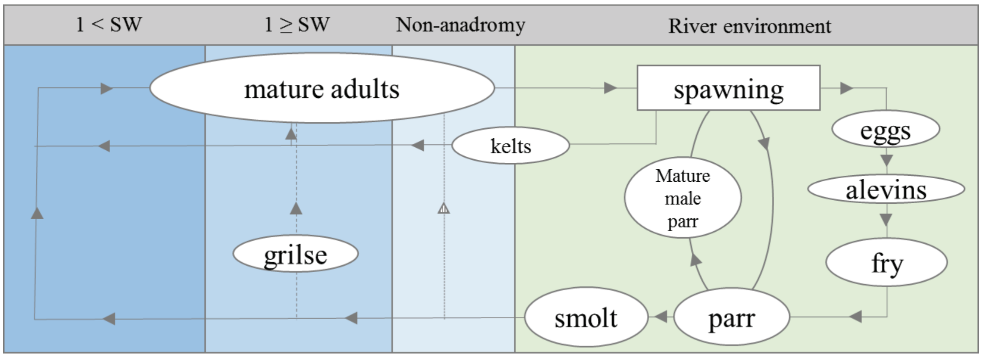

Figure 5. Conceptual illustration of the diverse and complex life-cycle and adaptations of the Atlantic salmon, reproduced from Verspoor et al. (2007). After spawning the eggs hatch and develop into alevins under the gravel in the redd, and when the yolksacks are consumed the fry escapes out of the redd and starts to feed. The fry develop in to parr. In the smoltification phase, physiological adaptations are developed for a more saline environment. Salmon staying only one year at sea (Sea Winter, SW) are referred to as grilse. Kelts are individuals that survive spawning and may migrate back to the sea and return to spawn once more. "Non-anadromous adaptations" refers to the land-locked populations (e.g. in Lake Vänern, Sweden) where the smolts migrate to lake environments instead of the sea.

The Atlantic salmon spawns in freshwater rivers during September-February depending on the latitude of the home river. Salmon typically return to their natal rivers with high precision, a so-called homing behaviour (Vladic & Petersson 2016), and only a small proportion of the population stray to other rivers (Aas *et al.* 2010). Thus, each spawning river constitutes of populations with ecological and genetic adaptations that are different from populations spawning in other rivers. During the spawning period, mature females construct nests or redds, where they deposit eggs that are fertilized by one or several males. Since the spawning period is long for most populations, late arriving females might use existing redds for their egg-deposition, and it is therefore common that redds may contain eggs from more than one female and several spawning events, in rivers where spawning habitats are spatially limited (Taggart *et al.* 2001). Aggressive behavior is common amongst males, competing for females. Even though aggression among females is uncommon, such competition might also occur when suitable spawning habitats are limited (Verspoor *et al.* 2007).

Depending on temperature, the eggs hatch after 70-160 days. After hatching, the salmon first develop into alevins which consume their yolksack under the gravel while maturing to free-swimming fry, which with increasing size eventually become parr. As parr, the salmon remain in the freshwater environment for 1-8 years until they undergo physiological adaptations and morphological changes suited for a life in marine environments (Aas *et al.* 2010). This phase is called smoltification and the smolts migrate to saltwater where they mature and eventually (after 1-5 years) return to their native river to generate the next generation. Although most individuals of Atlantic salmon share the marine life stage, some populations may stay their entire life in freshwater (e.g. landlocked lake populations in lake Vänern, Sweden, and Ladoga, Russia), whereas in other populations some individuals just make short coastal salt- or brackish water migrations (Webb *et al.* 2007). In contrast to most species of Pacific salmon (*Oncorhynchus* spp.), the Atlantic salmon is iteroparous, meaning that the spent adults may survive and potentially spawn several times (Fleming 1996). Roff (2016) suggests that the phenotypic plasticity in Atlantic salmon populations would include a proportion displaying semelparity, and that this life-history trait is a result of both genotype and the environment. Repeated spawning behaviour is most common among females, since males invest extensive energy in their territorial spawning behavior. Adults that survive spawning are termed kelts or repeat spawners (i.e. if they return to spawn once more).

Males may sexually mature already in the parr stage and reproduce early in their life-cycle. However, females will not usually actively mate with such small males. Instead, these early maturing parr males ("precocious males") adopt a "sneaker" or satellite spawning behavior, intruding on a spawning pair of anadromous salmon (Myers & Hutchings 1987). These precocious males may become smolts and migrate to the marine environment, returning to spawn as adults, or stay at the mature parr stage and spawn next spawning season as a satellite male again (Fleming 1996). Some Atlantic salmon return to spawn after just one season at sea. These smaller mature individuals, which are mainly males, are termed grilse.

As parr, the salmon lives solitarily, and their territorial behavior is essential in terms of increasing individual growth rate and survival. However, smolts in the same watershed often tend to synchronize their downstream migration before the sea entering (Stewart *et al.* 2006). This migratory pattern seems to be important for the survival rate of the sea-entering phase of the Atlantic salmon, where grouping or shoaling behavior might work as an anti-predator strategy (Aas *et al.* 2010). Shoaling is also observed in the marine post-smolt stage and later, although little is known about the post-smolt part of the life-cycle and most data comes from recaptures of tagged individuals or other indirect information (e.g. (Palm *et al.* 2008)). In the sea the principal source of natural mortality is suggest to be density independent factors that vary spatially and temporally (Klemetsen *et al.* 2003). The majority of this natural mortality occurs in the first few months after entering the sea, during the so-called post smolt phase (Verspoor *et al.* 2007).

4.2 Sea Trout

Sea trout is an anadromous life-history adaptation of brown trout (*Salmo trutta*) occurring in rivers with free access to the sea (Klemetsen *et al.* 2003). In many aspects the biology of sea trout is similar to that of Atlantic salmon. However, the life-history is more complex and highly variable (Elliott 1994; Baglinière & Maisse 1999). Compared to the salmon, sea trout often undertakes shorter marine or brackish water migrations that might be just over the summer or over two years in saltwater (Jonsson & Jonsson 2002). For some populations in the Baltic Sea, otolith analysis has revealed individuals where no freshwater phase was detectable, indicating potential spawning close to the river mouth where juveniles migrate to the sea in a very early stage (Limburg *et al.* 2001).

Another adaptation that has been observed for anadromous trout is that it may migrate to brackish water already as fry or parr (Landergren 2001), and then potentially stray to other rivers for further maturation (Degerman *et al.* 2012). The flexibility in the habitat niche of sea trout has made it possible for the species to use small creeks that potentially dry out as spawning habitats, due to the offspring adaptation to escape to coastal areas under harsh conditions (Järvi *et al.* 1996; Landergren 2001). Juveniles of sea trout are highly territorial (Elliott 1994), and dominant individuals may outcompete fish that shares the same habitats, both intra- and interspecific (Kalleberg 1958). Another main difference in sea trout compared to salmon is that proportions of the same population might migrate to the sea whereas others stay in the river their entire life (Jonsson 1989). This life-history adaptation is influenced by different factors, such as: distance to the sea (Rohtla *et al.* 2017), migration barriers (Jonsson 1982), and individual growth rate (Elliott 1994). In populations where both stationary and migrating individuals are present, females are overrepresented in the sea migratory proportion of the spawning stock (Elliott 1994).

4.3 Baltic Sea populations

The salmon in the Baltic Sea belongs to the same species (*Salmo salar*) as salmon in the North Atlantic, but it is genetically distinct from salmon in other regions (Verspoor *et al.* 2007). In the Baltic Sea there are nearly 40 rivers that have naturally reproducing salmon, which could be compared with around one hundred rivers that comprised naturally reproducing salmon in the past (ICES, 2017).

The wild Baltic salmon stocks was heavily degraded during the early 1990’s, due to overexploitation, historical hydropower construction (Koljonen 2001), destruction of spawning and nursery river habitats and disease (mainly “M74”; see below) (Asplund *et al.* 1999; Pickova *et al.* 2003). However, the ICES Baltic Salmon and Trout Assessment Working Group (WGBAST), has reported an increase in total wild salmon production since during the last decade, especially for some of the larger rivers in the northern Baltic Sea (ICES, 2017). This is mainly a result of reduced exploitation rates and conservation efforts to restore spawning habitats. Even if there has been a positive trend in smolt production for some wild Baltic Sea salmon populations, recent reports indicates an increase of the M74-syndrome that might affect future production (ICES, 2017). M74 is a reproductive disorder caused by thiamine deficiency. Low thiamine levels results in fry mortality and brain-damage to juvenile salmon, and the deficiency is suggested to reflect overconsumption among adults at sea of young sprat (*Sprattus sprattus*) which have a low thiamine concentrations in relation to their energy content (Keinanen *et al.* 2012). M74 affecting salmon in nature is hard to study and its prevalence in wild stocks has to be indirectly estimated via reports of fry mortality and thiamine content in unfertilized eggs from salmon at hatcheries (ICES, 2017). The Baltic sea trout stocks have severely declined, and in many rivers the natural reproduction has been completely lost, and todays recruitment of sea trout stems from only a few rivers, where the smolt production is considerably low compared to the estimated potential (ICES, 2017). This decline is mainly due to habitat loss and overexploitation (ICES, 2017). Catch-data from fisheries are sparse and it is unknown if current fishing rates allows the sea trout stocks to rebuild (Whitlock *et al.* 2017).

Since the 1950’s there have been extensive supplementary releases of hatchery-reared salmon and sea trout in the Baltic Sea, mainly as smolts. These releases are aimed mainly to compensate for the loss of wild populations due to hydropower exploitation of rivers (Ackefors *et al.* 1991). Last year (2016), 4.5 million salmon smolts were released, corresponding to a little more than half of the estimated total smolt production in the Baltic Sea (ICES, 2017). However, the releases of reared salmon and sea trout smolts has over time led to an intensification of coastal and river fisheries, using traps and gillnets generating increasing fishing mortality in coastal areas.

For the Baltic sea trout stocks the increasing coastal fisheries is thought to be one of the main reasons for the low abundance of wild sea trout, since sea trout utilizes these costal habitats as post-smolt feeding grounds (Degerman *et al.* 2012). Sea trout is not only fished as a target species in small-scale fisheries and recreational fishing, but it is also a common bycatch in other fisheries, mainly gillnet fishing for whitefish in the Gulf of Bothnia (ICES, 2017).

For the Baltic salmon stock assessment, information from different sources and life-stages are needed. The data regularly collected and available for this assessment can be categorized as:

- River surveys: parr density (electrofishing), smolt trapping, monitoring of spawning runs and river catches;

- Sea surveys: catch data, fishing effort data and catch composition data;
- Joint river and sea surveys: tagging data (tagging in rivers, recaptures from sea and river fisheries).

Moreover, the Baltic salmon and sea trout are monitored under the Data Collection Framework (DCF), which is an EU framework for the management of fisheries, where member states collect, manage and make data available to EU and bodies giving scientific advices for fisheries management. Even though commercial fisheries constitutes the majority part of the catch of salmon, recreational and non-commercial fishing are estimated to account for a substantial part of the total fisheries mortality (ICES, 2017). However, since there is no legislation requiring reporting of catches from recreational fishing, the recreational catch proportion is probably underestimated, and missing data are common in recreational fisheries data (Whitlock *et al.* 2017). With an increasing popularity of particularly off-shore trolling, there is a challenge for the future to obtain and collect data from recreational fishing. The highest proportion of fishing mortality for sea trout, probably stems from the increasing popularity in recreational fishing with nets and rods in both coastal areas and in river environments, probably to a higher extent than for salmon. With a Bayesian statistical approach accounting for reporting uncertainties for recreational fisheries, Whitlock *et al.* (2017) suggest that recreational fisheries mortality of sea trout might be equally or even more pronounce compared with professional fisheries.

4.4 Management of Baltic Sea salmon and sea trout

The management of the Baltic salmon and sea trout stocks is assessed using an age structured full life-history model using a Bayesian statistical framework (ICES, 2014). Since the salmon and sea trout life-cycle is complex and data for many stocks are sparse, the Bayesian statistical approach is highly suitable for stock assessment models, since uncertainties in the data will be quantified and presented as probability distributions. Moreover, it also allows incorporation of a diverse range of data, and scientific knowledge about the ecology of the targeted species can be used as prior probability distributions for the parameterization of the model (Walters & Martell 2004). Another advantage of Bayesian statistics is that both historical status and predictions for future stock development under different management goals could be estimated with the posterior probability distribution. For example, the Baltic salmon stocks are managed based on MSY (using a Beverton-Holt stock-recruitment model) with the aim of attaining at least 75% of the potential smolt production capacity (PSPC) (ICES, 2017). With a Bayesian statistical approach the output from the stock assessment model will for example give the probability of achieving at least 75% of the PSPC under different management approaches.

4.5 Density-dependent and –independent processes in salmon and sea trout

Density-dependent processes have been extensively documented for salmonid fishes in general and Atlantic salmon in particular, using data modelling (Hedger *et al.* 2013), field observations (Finstad *et al.* 2009; Foldvik *et al.* 2010, 2016) and experiments (Einum *et al.* 2006, 2011a; Finstad *et al.* 2007). The majority of the natural mortality occurs in the early life-stages (Elliott 1994; Baglinière & Maisse 1999; Verspoor *et al.* 2007; Aas *et al.* 2010; Einum *et al.* 2011b). Eggs are most vulnerable during the period from fertilization to the eyed embryonal stage where mechanical perturbation caused by other spawners, flooding and other environmental factors may influence the survival rate (Haddon 2001; Verspoor *et al.* 2007). Moreover, eggs and alevins displaced from the gravel suffer high predation mortality from older parr and other fish species in the river (Verspoor *et al.* 2007). The fry stage is associated with high density-dependent mortality (Elliott 1994; Klemetsen *et al.* 2003; Aas *et al.* 2010) mainly driven by intraspecific competition for food (Kalleberg 1958; Elliott 1994). This competition is strongly connected to their territorial behavior almost immediately after emergence from the redds, and induces dispersal to suitable feeding grounds, where the strongest competitors gain the best habitats and the outcompeted individuals have to disperse the longest distance (Kalleberg 1958; Einum *et al.* 2011b). Fry that emerge early from redds often obtain the best feeding grounds resulting in a lower individual density-dependent mortality (O'Connor *et al.* 2000), given that there is a match between emergence time and food abundance. The fact that the majority of density dependence occurs in the earliest life stage combined with the short spatial dispersal patterns of juvenile salmon and sea trout, suggests that density-dependent process may be strongest at fine temporal and spatial scales (Einum & Nislow 2005; Foldvik *et al.* 2010; Einum *et al.* 2011b). However, stock assessment models used for most salmonid fishes do not account for the local density dependence, potentially leading to bias in estimates of stock-recruitment relationships and worsened predictive ability of stock assessment models.

Interspecific competition between sea trout and salmon is likely weak in the parr and late juvenile life stages (Berg *et al.* 2014), where juvenile sea trout often utilize deeper slow-current feeding grounds, compared with salmon, that throughout the pre-recruit phase often use stronger current habitats (Baglinière & Maisse 1999). This difference in habitat preference is due to morphological adaptations in salmon allowing deflection of strong water-movement (Jones 1975). However, studies indicate that there is a potential niche overlap in rivers with similar characteristics and in the earliest life stage with potential niche overlap. Where interspecific competition is observed, trout is often favored due to a more pronounced territorial aggressive behavior compared with salmon (Kalleberg 1958; Van Zwol *et al.* 2012), which is connected to the defense of feeding- and refuge areas. Most studies regarding interspecific competition between salmon and trout has been made on relatively old juveniles often in the parr stage (Kalleberg 1958; Berg *et al.* 2014). However, as mentioned before, the strongest intraspecific density-dependent mortality may occur in the earliest juvenile stage, at fine spatial and temporal scales, thus, more studies covering interspecific competition in the fry life stages are needed. Moreover, no studies to date, have focused on interspecific competition at different densities, and how it may affect dispersal or mortality in the two species.

The stock assessment model for Baltic Sea salmon stocks assumes "whole-river" density dependence during the pre-recruited life stages (ICES, 2014). Meaning that the density- dependent element in the stock assessment model is based on a total density-dependent process, which might violate patterns indicated by earlier studies, showing that local density-dependent processes are more prone to regulate salmon populations (Einum *et al.* 2011a, b). Moreover, spawning individuals of salmon do not distribute uniformly in the river (Finstad *et al.* 2013) or follow an ideal free distribution (Fretwell & Lucas 1969), so dependent on the distribution pattern of the spawning stock this "whole river" density-dependent assumption might over- or underestimate the recruitment potential when local scale processes are ignored (Einum *et al.* 2008). Finstad *et al.* (2013) showed that the preferred spawning sites of Atlantic salmon were positively correlated to the abundance of other spawners and spawning sites used previous years as spawning sites. Moreover, there was a negative correlation between distances from previous used spawning sites to new suitable spawning sites. This indicates that spawning of salmon occurs in aggregations or in spawning sites that has been used before, and spawning dispersal to further located new spawning sites may therefore take several generations before utilization. Giving this, an increase in spawner abundance one year may not direct generate a higher recruitment.

5 Summary

Management of exploited natural populations requires extensive knowledge of the organism's ecology and life-history in order to achieve sustainable harvest. Even if regulatory processes are well-studied for many exploited populations, the ability to predict population development will be poor if the effects of these processes on different scales are overlooked (Einum & Nislow 2005). Fish are no exception, and like many other organisms the majority of the density-dependent regulation occurs during the early life-stages (Ricker 1954; Beverton & Holt 1957), and compensatory density-dependent mechanisms allows sustainable removal of individuals from a population (Schaefer 1954). For most salmonid fishes, density-dependent processes are constrained to a river environment, where suitable spawning and nursery habitats are heterogeneously distributed. This will generate locally and temporally high aggregations of individuals during the pre-recruited phase, inducing density-dependent processes that will influence recruitment in the population. A rising number of studies on density dependence show that juvenile salmonid fish in the earliest life-stages disperse over small distances (25-100m) from the spawning grounds, and that density-dependent processes act on fine spatial and temporal scales (Einum & Nislow 2005; Einum *et al.* 2008, 2011b, b; Teichert *et al.* 2010, 2017). Finstad *et al.* (2013) showed that Atlantic salmon preferred the same spawning grounds as other spawners, and spawning grounds used in previous years, over "new", unoccupied spawning grounds. This spawning ground preference indicates that density-dependent mechanism may act even at low spawning stock abundances, where spawning grounds may be utilized beyond local carrying capacity before dispersal to unoccupied or low density spawning grounds. Understanding and incorporate these processes in stock assessment could generate better estimates of the population dynamics and improve conservation efforts.

The stock assessment model for the Baltic salmon stocks assumes a whole-river density dependent effect (ICES 2014). Even if studies indicates spawning ground preference and the strength of local density-dependent processes for salmon (Einum *et al.* 2006; Teichert *et al.* 2010; Finstad *et al.* 2013), the potential magnitude of the bias in stock assessment models assuming whole-river density-dependent processes has not been quantified. In my thesis work I will explore the implication of local density-dependent dynamics for inference about the relationship between spawning stock size and recruitment. This is an important aspect of fisheries management since fishing mortality rates are usually set on the basis of stock assessment models, and overlooking the local scale of density dependence could potentially result in overexploitation.

Initially, I will explore the potential bias in parameter estimates from stock assessment models assuming whole-river density dependence, in environments where local underlying processes constitutes the density-dependent dynamics. This will be done by estimating stock-recruitment parameters from simulated data assuming different spawning dispersal patterns with local stock-recruitment dynamics and density-dependent processes, and compare the parameter estimates with stock-recruitment models assuming whole-river dynamics. Potential bias. Potential bias in parameter estimations caused by the ignorance of local population dynamics will be quantified.

In my second paper, I will check if local density-dependent effects could be detected in juvenile density time series data. There are large volumes of available data for salmon and sea trout from Sweden, both from the juvenile (e.g. electrofishing data, smolt trapping, pit-tags etc.) and the adult (e.g. fish ladder counts, Carlin-tagging etc.) life stages. These data comprise long-term periods and stock abundances ranging from relatively low to high densities. I will analyze existing empirical data from parr electrofishing surveys, testing for patterns in salmon parr density in space and time. The results will be compared to predictions of spatio-temporal development of parr densities from paper 1.

In my third paper, I will explore the relative importance of interspecific competition of salmon and sea trout on a small spatial scale. These two species could potentially co-occur during the early life-stages, since the two species to some extent share the same preference for river habitats (Heggenes *et al.* 1999). Earlier studies have explored this competition process but mostly using fish in a relatively late phase of the juvenile life-stage (e.g. Kalleberg 1958; Skoglund *et al.* 2012; Puffer *et al.* 2017), where density-dependent mortality most likely already has occurred. In my experiments on a fine spatial scale (4 x 0.6 x 0.25 m), I will study the interspecific competition at different densities and ratios of the two species, in the earliest life-stage (just after emergence), to be able to evaluate any potential species-specific advantage. This scale and life-stage is most relevant for the density-dependent mortality of the two species (Elliott 1994; Einum & Nislow 2005; Einum *et al.* 2011b; Skoglund *et al.* 2012). If there is a strong advantage for either species in this interspecific competition scenario, this indicates that this process might be necessary to account for in the existing stock assessment models. Moreover, this study would give more knowledge of the Baltic Sea trout life-history, a species that is gaining increasing attention in Baltic Sea fisheries management.

For the Baltic salmon stock assessment, recruitment (i.e. number of sea-migrating smolts) is only surveyed in six out of 30 assessment rivers, by smolt trapping. For most of the other rivers, wild smolt production is estimated from parr densities (electrofishing surveys). Using a hierarchical linear regression analysis, the parr to smolt corresponded parameters are transferred through hyperparameters from rivers with both smolt and parr surveys, to rivers that have long time-series of parr abundance data but lack smolt counting data (ICES 2014). Additional data in this model is river discharge, which is used as an explanatory variable for the slope of the linear model in each river. In my fourth paper, I would like to evaluate if and how additional information could be used in this model to potentially improve the parameter estimates. Other parameters that will be tested and is suggested to influence the survival of young salmon are: parr-length (Jonsson *et al.* 1998), habitat characteristics (e.g. shelter, Finstad *et al.* 2007, 2009) and temperature (Foldvik *et al.* 2015).

In my fifth paper, I will incorporate the potential updated knowledge, gained from my first four papers, and evaluate how this potentially could improve the existing full life-history population model for the Baltic salmon stock assessment. By including local density-dependent processes, studied in the four first papers, in the parameterization of the existing stock-assessment models, the potential increase in predictive power could be evaluated. If accounting for local density dependence improve the parameter estimates for the stock development, this would suggest that available data in the stock assessment work would perhaps be used in another manor, and perhaps using alternative monitoring methods existing today (e.g. electrofishing).

Extensive amount of research suggest that local density-dependent processes in salmon and sea trout populations is the most important scale determining the population dynamics (e.g. Elliott 1994; Einum & Nislow 2005; Foldvik *et al.* 2010; Teichert *et al.* 2010, 2017; Einum *et al.* 2011b, a; Finstad *et al.* 2013). Yet little implication of this is accounted for in the management of these populations. Population models missing key aspects of dynamic processes might under- or overestimate the production potential of certain fish stocks, and advising fishing mortalities that potentially might induce declines of natural fish populations. My thesis work will aim to explore the potential bias overlooking some of the local dynamics in the stock assessment work, and how monitoring data could best be used to inform the management of salmonid fish stocks.

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