Acta Universitatis Agriculturae Sueciae

Doctoral Thesis No. 2024:18
Faculty of Natural Resources and Agricultural Sciences

Population regulatory processes in the Baltic salmon (*Salmo salar*)

Stefan Skoglund

Population regulatory processes in the Baltic salmon (*Salmo salar*)

Stefan Skoglund
Faculty of Natural Resources and Agricultural Sciences
Department of Aquatic Resources
Uppsala

SLU
SWEDISH UNIVERSITY
OF AGRICULTURAL
SCIENCES

DOCTORAL THESIS
Uppsala 2024

Acta Universitatis Agriculturae Sueciae
2024:18

Cover: Eyed eggs from Atlantic salmon (*Salmo salar*)
(photo: Stefan Skoglund)
ISSN 1652-6880
ISBN (print version) 978-91-8046-300-3
ISBN (electronic version) 978-91-8046-301-0
https://doi.org/10.54612/a.58aq72nqq6

Swedish University of Agricultural Sciences, Department of Aquatic resources, Uppsala, Sweden

Print: SLU Grafisk service, Uppsala 2024

Population regulatory processes in the Baltic salmon (*Salmo salar*)

Abstract

Knowledge and understanding of population regulation is the foundation that allows for sustainable harvest of natural populations. In this thesis, I explore potential sources of bias in stock recruitment relationships resulting from potential spawning behaviours, and investigate alternative methods that can be used in order to evaluate population regulatory processes and improve estimates of stock-assessments of the Atlantic salmon (Salmo salar) in the Baltic Sea. I show that the spawner behaviour affects the stock-recruit relationship, and that estimates of recruitment and stock-recruit parameters in two common stock-recruitment functions might be biased. Further, I show that empirical data can be used in order to define the spawner behaviour. Using electrofishing data and spawner count estimates, I found that the underlying within-river spawner behaviour for salmon in River Byskeälven was most probably homing. I also provided an alternative method to predict length and age at smoltification for the Atlantic salmon, and show that this method can be used to predict smolt length and age distributions in rivers where only data of parr lengths are available. Lastly, I use experiments to explore the competition between juveniles of Atlantic salmon and trout (*Salmo trutta*). I find that the two species outcompete each other and that this relationship is not density-dependent but rather seems to be temperature-dependent, where trout is the stronger competitor in warmer temperatures compared to salmon that outcompete trout in colder waters.

The results in this thesis provides important knowledge and understanding of regulatory processes in Baltic salmon, which can be used to improve the stock assessments.

Keywords: population regulation, stock assessment, Atlantic salmon, density dependence, simulation, experiments

Populationsreglerande processer hos Östersjölax (*Salmo salar*)

Sammanfattning

I fiskeriekologi utgör förståelsen om populationsreglering fundamentet och är den process som möjliggör ett hållbart uttag från naturliga populationer. I denna avhandling undersöker jag potentiella källor till bias i beståndsanalyser, samt alternativa metoder som kan användas för att skatta effekten av populationsreglerande processer. Först studerar jag hur spridningsmönster av lekfisk påverkar beståndsuppskattningsparametrar och finner att beroende på spridningsmönstren hos lekfisken så kan det genereras bias i estimaten av rekrytering och rekryteringparametrarna i de två vanligaste beståndskattningsmodellerna. Detta kan introducera en högre täthetsberoende dödlighet än förväntat. Dessa modeller användes sedan på befintliga data för att definiera spridningsmönstret av lekfisk hos östersjölax (Salmo salar). Resultaten är i linje med andra studier som föreslår att laxen tenderar att även inom älven återvända till födelseplatsen för lek. Jag presenterar även en metod för att förutsäga vid vilken storlek och ålder som lax smoltifierar. Genom att använda längddata från stirr och smolt gick det att förutsäga vid vilken längd och ålder som laxen vandrar ut i havet. De parametrar som estimerades med denna metod kunde även överföras till närliggande älvar för att estimera storlek och åldersfördelningen av smolt baserat på endast stirrlängder. Genom experiment utforskade jag slutligen konkurrensen mellan lax och öring (*Salmo trutta*). Jag finner att de två arterna konkurrera ut varandra men att detta mönster inte är täthets beroende utan snarare temperaturberoende då öringen är den starkaste konkurrenten vid högre temperaturer och lax vid lägre. Resultaten i denna avhandling ger viktig kunskap och förståelse för regleringsprocesser vilka är viktiga vid beståndsanalyser..

Keywords: populationsreglering, beståndsuppskattningar, atlantlax, täthetsberoende, simuleringar, experiment

Dedication

To those who should have been here:
Mom *1952 –†1999
Jeanette *1980–†2020

Contents

List of publications

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

I. Skoglund S., Whitlock R., Petersson E., Palm S., Leonardsson K. (2022). From spawner habitat selection to stock-recruitment: Implications for assessment. Ecology and Evolution, 12: e9679

II. Skoglund, S.; Leonardsson, K.; Romakkaniemi, A.; Whitlock, R. Evaluating alternative spawner distribution models for Atlantic salmon (Salmo salar). (Manuscript)

III. Skoglund, S.; Whitlock, R.; Magnusson, K.; Leonardsson, K. Growth and smoltification of the Atlantic salmon (Salmo salar). (Manuscript)

IV. Skoglund, S.; Palm, S.; Söderberg, L.; Petersson, E. Competition between Atlantic salmon and brown trout juveniles after emergence. (Manuscript)

Papers I is reproduced with the permission of the publishers.

Peer-reviewed work not included in the thesis:

Sundin, J.; Persson, J.; Wickström, H.; Renman, O.; Skoglund, S. 2022. Evaluation of Sampling Methods for Maturation Stage Determination in the European Eel *Anguilla anguilla*. Marine and Coastal Fisheries 14:e10219

1. Introduction

Thomas Robert Malthus, an English economist and priest, suggested that the human population, if unrestrained, would grow exponentially until exhaustion of common resources limited further growth (Malthus, 1798). Even if a large part of Malthus' solutions to uncontrolled population growth would seem controversial and outdated today, he coined the concept of population regulation. Population regulation has since then become a foundation in ecology and biology, as it influences many processes observed in nature. Because population regulation determines the productivity and abundance of natural populations, knowledge of regulatory mechanisms is central in order to achieve long-term sustainable harvest rates of wild populations.

1.1 Population regulation

In ecology, a population is referred to as a group of organisms of the same species that are living and reproducing within a defined area (Relyea, 2021). In addition there are more specific sub-categorical definitions (e.g. sources and sinks (Pulliam, 1988)), but for the purpose of the present discussion, the term "population" will adhere to the basic concept as described in Relyea (2021).

Following Malthus (1798), three main factors regulate the abundance of a population: 1) persistence, where populations persists over time, 2) boundedness, where the variations in population abundance are bound between upper and lower (non-zero) limits, and 3) return tendency, where population abundance will decrease above a certain abundance threshold (e.g. carrying capacity), and increase when abundance is reduced (Hixon et al., 2012; Murdoch, 1994; Turchin, 2003). The mechanisms that regulate population abundance are widely divided into density-dependent (endogenous) and density-independent (exogenous) processes (Cherrett and Bradshaw, 1989; Murdoch, 1994; Sinclair and Pech, 1996; Turchin, 1999, 1995). The relative strength or importance of these two mechanisms on population regulation has been heavily discussed historically (Andrewartha, 1957; Andrewartha and Birch, 1954; Berryman, 2004; Milne, 1962; Murray, 1999; Reddingius and den Boer, 1970; Sinclair and Pech, 1996; Turchin, 1999). However, today most researchers in population ecology agree that both mechanisms influence population regulation, where the relative regulatory strength differs between populations and environments (Turchin, 1999). Importantly, both density dependence and density independence directly or indirectly affects one or more demographic rates in a population, which in turn influence population abundance.

1.1.1 Density dependence

Density dependence is one of the strongest driving forces in ecology and evolution, regulating and shaping organisms on both individual and population scales. Density-dependent regulation is influenced by various mechanisms, e.g. intraspecific competition (Svanbäck and Bolnick, 2007), predation (Abrams and Ginzburg, 2000) and/or diseases (Turchin, 1999). Intraspecific competition is per definition always density-dependent and ultimately affects survival and/or fecundity (Hixon et al., 2002; Rose et al., 2001), whereas predation and diseases could be both density-dependent and/or density-independent (Sinclair and Pech, 1996). However, interspecific density-dependent competition could also affect population dynamics. As an example, interspecific density-dependent competition could explain cyclic patterns in the abundance of species competing over the same limiting resources (Gamelon et al., 2019). Moreover, density-dependent interspecific competition often influences habitat use and drives niche and/or spatial separation of species (Hasegawa, 2016), which could indirectly influence survival and ultimately population abundance. It might therefore be of interest to evaluate not only density-dependent intraspecific competition, but also how density dependence affects interspecific competition.

Competition could be direct (interference; Case and Gilpin, 1974), or indirect (exploitation; Finstad et al., 2007), where the limited resource depends on the species and/or the life stage (Arcese and Smith, 1988;

Bergman and Greenberg, 1994; Bouchard et al., 2018; Brännström and Sumpter, 2005; Ford and Swearer, 2013; Montorio et al., 2018; Morris, 2003). Regulation via density dependence is often restrained to one or a few life-stages, and for many species occurs in the initial life-stages (Andersen et al., 2017), whereas regulation in the adult life-stages are thought to be mainly driven by density-independent processes (Turchin, 1999). Moreover, density dependence often occurs at small spatial and temporal scales (Einum et al., 2011; Fernández-Bellon et al., 2016), where the observed effect of density dependence is the sum of processes acting on different scales (Relyea, 2021; Walters and Martell, 2004). It is therefore important to gain knowledge of density dependence over different temporal, spatial and demographic scales in order to fully understand the processes affecting population dynamics.

Within the concept of density dependence, compensation is perhaps one of the most important mechanisms for managed populations (Rose et al., 2001). Compensation is the mechanism whereby an increase in population abundance generates a decrease in productivity, whereas a reduction in population abundance would tend to increase productivity through density-dependent processes (Rose et al., 2001; Turchin, 1995). This means that the productivity of a population (i.e. net population increase) varies with population abundance. There are several population models including compensatory factors, of which the logistic growth model (Verhulst, 1838) is perhaps the most widely-used. The logistic growth model describes population development over time, where the maximum abundance is restrained by some density-dependent limit (e.g. carrying capacity). Even if the intrinsic growth rate (i.e. number of offspring produced per reproducing individual) is constant, the population growth will vary with population abundance, since at high abundance the population growth rate will be reduced due to density dependence (Fig. 1). Thus, the net increase in population abundance (population growth rate) also varies over the range of population abundance (Fig. 1) (Sibly and Hone, 2002).

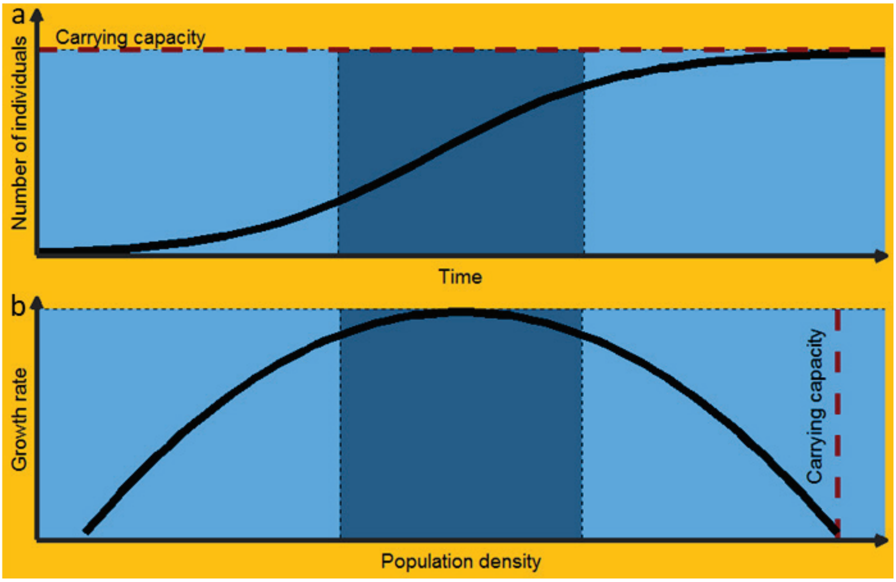


Figure 1. Population growth over time described with a logistic growth model (a). Population growth rate (net increase in abundance) is low at low population abundance and increases with increasing abundance until the inflection point is reached (carrying capacity/2), after which the growth rate decrease and becomes zero when population abundance equals the carrying capacity (b).

1.1.2 Density independence

The term "density-independent" is used to refer to processes that act irrespective of a population's abundance. This could be through e.g. temperature, habitat area, interspecific competition etc. Even if Turchin (2003) and Hixon et al. (2012) claim that regulated populations must exhibit density-dependent regulation in at least one demographic rate (e.g. birth or deaths), density-independent factors can still influence population regulation. For example, if interspecific competition and/or temperature, or the interaction of both, influences size at age (Thunell et al., 2022), this could regulate populations if reduced size would affect the reproductive output (i.e. via fecundity, (Honěk, 1993) or mortality (Zimmermann et al., 2021), and thereby ultimately the population abundance. In Atlantic salmon (Salmo salar) it has been shown that the growth rate in young parr was affected by temperature and the photoperiod, which in turn influenced the size and age at smoltification (Imsland et al., 2014). Note that growth, not only in salmon parr, but for other species could also be density-dependent (Eikeset et al., 2016; Einum et al., 2008; Imre et al., 2005; Vincenzi et al., 2012) . Age and size at smoltification may also influence the post-smolt survival (Jutila et al., 2006; Letcher et al., 2002) and the fecundity of returning spawning individuals (Friedland and Haas, 1996), and thereby population abundance. Moreover, density independence may also regulate populations if environmental conditions are altered, and suitable habitat areas are reduced, inducing increased density-independent (interspecific) and/or –dependent (intraspecific) competition (Morris, 2003). Since density-independent processes affects population regulation, it is important to monitor and include these processes when assessing natural populations.

1.1.3 Population regulation and sustainable harvest

Sustainable exploitation of natural populations (sustainability) can be defined as long-term harvest of a population that does not introduce a significant reduction in population abundance over time. Management of harvested natural populations depends on compensation that theoretically would allow sustainable outtake of individuals (Haddon, 2001; Quinn and Deriso, 1999; Walters and Martell, 2004). This is possible since a reduction in the abundance of a population is expected to generate an increase in the population's growth rate due to compensation (Lorenzen, 2008; Rose et al., 2001). Achieving sustainable harvest requires knowledge of population dynamics and key factors (both density-dependent and –independent) that influence the productivity of the harvested population.

1.2 Fisheries ecology and stock assessment

Fishing is one out of few human activities where natural populations are exploited on a commercial scale. In fisheries ecology the main goal is to describe and assess the population dynamics and regulatory factors of exploited fish populations (Walters and Martell, 2004). The management unit is often defined as a stock, which may constitute of several local populations, and where data from large spatial and temporal scales are used in the stock assessment (Haddon, 2001; Hixon et al., 2012; Kareiva et al., 1990).

A common overarching target for managed fish populations is to maximize the long term yield, e.g. achieving maximum sustainable yield

(MSY) (Hilborn et al., 2015; Vert-pre et al., 2013). The harvest rate that maximizes yield is dependent on the productivity of a stock (potential rate of stock increase) which is estimated using stock-recruitment models where information of the regulatory mechanisms are central components (Beverton and Holt, 1957; Quinn and Deriso, 1999; Ricker, 1975; Walters and Martell, 2004). In order to reach management goals it is therefore important to obtain knowledge of the mechanisms that regulate productivity. However, fitting statistical models to the relationship between the spawning stock and the subsequent number of recruits is one of the most error prone procedures in fisheries ecology (Conn et al., 2010; Lorenzen, 2008; Marshall et al., 2006; Needle, 2002; Sakuramoto, 2005). Suggested sources of bias include observation and process errors (Hulson et al., 2011; Linton and Bence, 2008; Walters and Martell, 2004), shifts in productivity regimes (Gilbert, 1997; Vert-pre et al., 2013) and time-series bias (Walters, 1985). Moreover, insufficient knowledge of regulatory processes or violation of model assumptions might also introduce bias in stock recruitment estimates (Cadrin et al., 2023; Pulkkinen and Mäntyniemi, 2013). Therefore, more knowledge of productivity regulatory processes is typically warranted.

The two most commonly used stock-recruitment models applied in stock assessments are the stock-recruit functions developed by Beverton-Holt (Beverton and Holt, 1957) and Ricker (Ricker, 1975) (Fig. 2). Both of these stock-recruitment functions include the maximum reproductive rate which is the number of recruits per unit spawning stock at low stock sizes (or the initial slope, Myers et al., 1999) which is density-independent, as well as density-dependent regulation, but differ in terms of the regulatory response to changes in abundance. The Beverton-Holt function describes an asymptotic density dependent response whereas the Ricker function includes over-compensation, which, for example could be introduced via cannibalism or superimposition of spawning grounds (Ricker, 1975). In general, these two models produce reasonable descriptions of the stock productivity for many fish species, but the resulting accuracy in estimates of the parameters and the stock-recruitment relationship depends on the knowledge of underlying regulatory processes and that the data used to estimate the functions are unbiased.

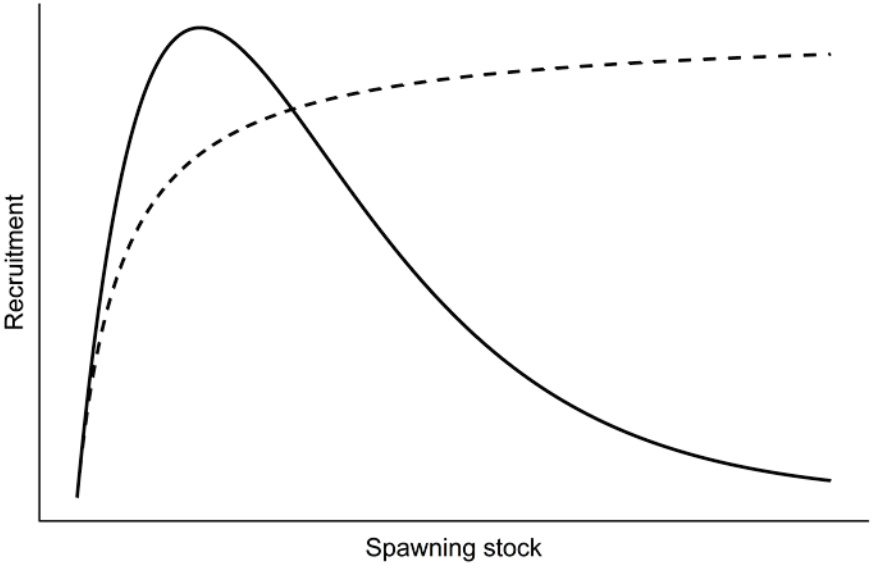


Figure 2. Conceptual illustration of the Beverton-Holt (dashed line) and the Ricker (solid line) stock-recruitment functions.

1.3 The Baltic salmon

Baltic salmon populations, i.e. populations of Atlantic salmon (Salmo salar) in the Baltic Sea, are genetically divergent from other Atlantic salmon populations (Säisä et al., 2005). In addition, there is a high degree of genetic structuring between populations in different rivers (Palmé et al., 2012). Within the Baltic Sea, the anadromous populations form three clear genetic groups corresponding to rivers in the northern (Gulf of Bothnia), eastern (Gulf of Finland and eastern Baltic Main Basin), and southern regions (western Baltic Main Basin). This suggest that the colonization of the Baltic Sea by at least three glacial lineages (Säisä et al., 2005).

The Baltic salmon shares a multitude of life-history traits with other Atlantic salmon populations (Aas, 2011). It is anadromous, spawning in freshwater rivers, after which it feeds and grows in the Baltic Sea. After 1-6 years (sea winters, SW) in the ocean, maturing spawners return to the natal river with high precision, which is reflected in genetically distinct populations among rivers and sometimes also within rivers (Miettinen et al., 2021).

Fishing for adult Baltic salmon occurs both at sea (offshore and along coasts) and in rivers. Each river population of the Baltic salmon is assessed individually, but in the sea fisheries are exploiting a mixed-stock comprising different populations originating from different rivers (International Council for the Exploration of the Sea, ICES, 2019). The wild Baltic salmon stock had become heavily reduced in the early 1990's due to a long-term combination of large-scale hydropower exploitation, degraded river environments (e.g. due to log floating), high harvest rates in the sea and reproductive disturbance caused by diseases such as "M74" or "early mortality syndrome" (Honeyfield et al., 2005; Koljonen, 2001). However, since the mid-1990s, especially reduced harvest rates have resulted in a recovery of several of the remaining wild river stocks, although some populations still have low abundance levels (especially populations in the southern Baltic sea, ICES, 2023). The main problem with mixed stock management is that all populations share the same fishing quota and selective fishing in the sea of healthy (wild or hatchery reared) populations is typically not possible (ICES, 2023).

1.3.1 Lifecycle

The lifecycle of the of the Baltic salmon is similar to that of the Atlantic salmon and has been well studied and many of the population regulatory mechanisms are well known (e.g. Aas, 2011). In common with other Atlantic salmon populations, Baltic salmon mature in the sea and migrate back to natal rivers to spawn in freshwater. The majority of Baltic salmon individuals are assumed to be semelparous (spawning once) in the stock assessment model. However, there are individuals that might spawn several times (ICES, 2023). A study made on Norwegian populations of Atlantic salmon show that between 0 and 26% of the salmon females were repeat spawners (Persson et al., 2023), which is perhaps also true for the Baltic Salmon. Salmon females select a suitable spawning area where they construct a spawning nest in the gravel where eggs are fertilized and buried in the gravel (Aas, 2011). After hatching, the fry grow and become parr. Parr spend 1-5 years in the rivers before developing into smolts. Smolts migrate to the ocean and mature until spawning migration back to the natal river (Aas, 2011).

The main density-dependent regulation of the Baltic salmon occurs in the early life-stages, often between the fry- and parr-stage (Einum et al., 2011, 2006), whereas smolt and adult mortality (ocean life-stages) are mainly regulated via density-independent factors (Jonsson et al., 1998). Moreover, the data availability for the Baltic salmon is good, including long-term data covering both juvenile and adult life stages.

However, there are still knowledge gaps, where an increased understanding of the population regulation of the salmon might improve population modelling and stock assessment (ICES, 2023). In particular, knowledge of how spawning individuals distribute within rivers is scarce. Also, the lack of within-river information about how the spatial distribution of spawners might influence stock-recruitment dynamics is also limited. In addition, knowledge about age and size at smoltification, important population regulatory factors, is today limited to a few rivers in the stock assessment. There is also a lack of information about how the initial density-dependent regulation in the earliest life-stage of Baltic salmon might be affected by interspecific competition from the closely related brown trout (Salmo trutta).

2. Aim of the thesis

The aim of this thesis is to explore different processes and mechanisms that influence population regulation, using Baltic salmon (Salmo salar) as a model species. More specifically the aim of the thesis will answer the following questions:

Does the spatial distribution of spawning individuals influence the stock-recruitment relationship, and does violation of the assumption of the underlying spawner behaviour introduce bias into estimated stock-recruitment functions? (**Paper I**).

Can spawner and juvenile abundance data be used to evaluate the underlying spawner distribution behaviour of salmon, when comparing different theoretically plausible behaviours? (**Paper II**).

Can length and age at smoltification of salmon be estimated from length measurements of parr and smolts, and can parameter estimates within a reaction norm from one river be transferable to other rivers where only parr length data are available, in order to predict length and age at smoltification? (**Paper III**).

Does density affect interspecific competition between salmon and brown trout in the initial life stage after emergence? (**Paper IV**)

3. Methods

In this thesis, I have used a wide range of methods stretching from theoretical computer simulations (**Paper I**), to estimation within a Bayesian statistical framework (**Paper II**), to non-linear regression analysis (**Paper III**), to experiments (**Paper IV**). In Paper II and Paper III, I also used empirical data to explore different population regulatory processes (spawner behaviour of salmon and length and age at smoltification, respectively). Since **Paper I** and **Paper II** are based on the same spawner behaviour models they are described together.

3.1 Spawner behaviours

To evaluate how the distribution of spawners might affect the stock-recruitment relationship and parameters estimated in stock-recruitment functions, I first defined and modelled four possible spawner behaviours: Habitat Quality distribution (Hab Q), Ideal Free Distribution (IFD), stepwise distribution and a random distribution. These four spawner behaviours were used in Paper I, and all except the random behaviour were also used in Paper II, in which the random spawner behaviour was exchanged for a natal homing (homing) spawner behaviour. All spawner behaviour models are described in detail in **Paper I** and **Paper II**. In short, the five different spawner behaviours can be described as:

- The Hab Q spawner behaviour is based on the assumption that the local carrying capacity is the main habitat selection cue. This means that under a Hab Q spawner behaviour, spawners will distribute proportionally to local carrying capacities (Ki) (Fig. 3), where i indicates the local spawning site (Fig. 3).

- The IFD theory is when reproducing individuals adjust local abundance in order to obtain the maximum possible fitness (Fretwell and Lucas, 1970). The IFD include fitness and thereby perceived juvenile survival in the spawner behaviour. This was modelled based on Ki, egg to young-of-the-year (YOY) survival (S0) and local migration mortality of smolts (S1i) (Fig. 3).

- The Stepwise spawner behaviour was based on the study of Atlantic salmon by Finstad et al. (2013), suggesting that social attraction would generate higher local spawner abundance and that utilization of adjacent spawning grounds is positively correlated with increasing local spawner abundance. We modelled the stepwise function so that the spawning site with the highest S1i was used first, until a threshold density (based on Ki) was reached, followed by the spawning site with the second highest survival (S1i), and so on until all spawning sites were utilized (Fig 3).

- The Random spawner behaviour was modelled as complete random distribution of spawners among all sites.

- The Homing behaviour was modelled as a propensity to return to the natal spawning site. The natal spawning site had the highest probability of being selected, while adjacent spawning sites were selected with a decreasing probability based on the distance from the natal site (Fig. 3).

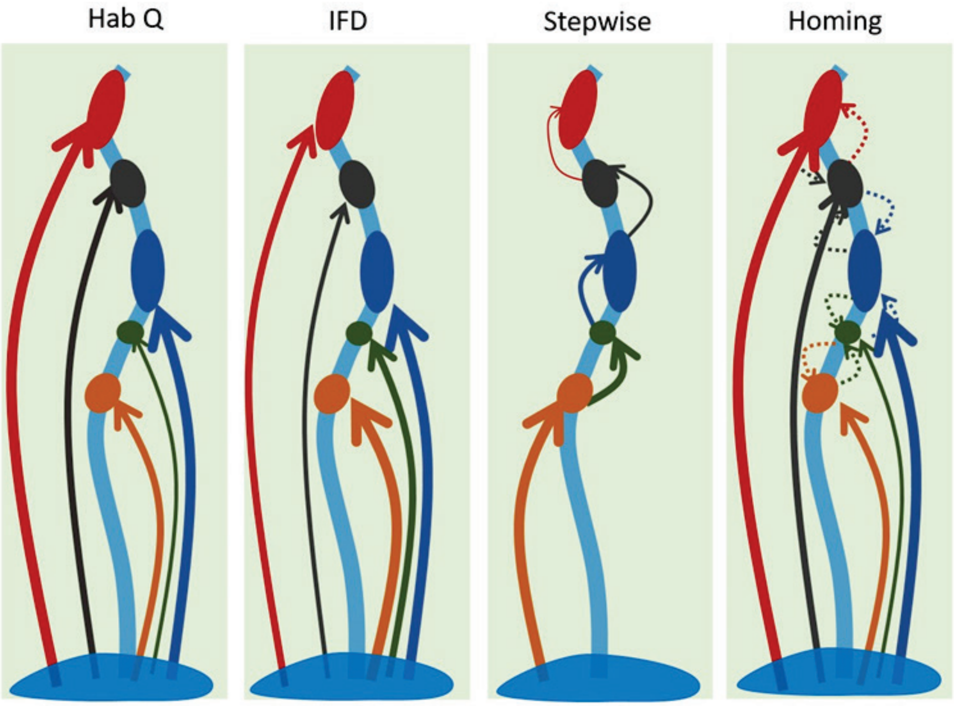


Figure 3. Four models of spawning distribution among five hypothetical spawning sites: habitat quality (HabQ), ideal free distribution (IFD), stepwise, and homing (random model not shown). Coloured arrows represent movement of spawners onto the spawning sites where the line width is scaled in correspondence with the number of spawners inhabiting the site, which is proportional to habitat size for the HabQ model and total fitness including habitat size and survival of juveniles during downstream migration of the IFD model. In the stepwise model, spawning areas are inhabited sequentially based on distance, and in the homing model spawners return to their natal sites with an estimated propensity for straying to neighbouring sites.

3.1.1 The influence of spawner behaviour in stock assessment

Population simulations were used to explore how the violation of the assumption of the underlying spawner behaviour would influence the estimate of recruitment, survival rate and carrying capacity in a river. In **Paper I,** population dynamics were simulated based on local spawning site characteristics (Ki, S1i and S0) that were sampled from realistic probability distributions. Using the same set of local spawning site characteristics for all spawner behaviours (Fig. 3), females were distributed over all available spawning sites (n=5) in a model river, based on the different spawner behaviours. In each spawning site and for each simulation round (n=1000), the local recruitment was calculated based on either a Beverton-Holt or a Ricker local stock recruit function. The total number of recruits were then calculated as the sum over all local spawning sites and compared with the predicted number of recruits and parameter estimates based on two commonly used stock recruitment functions (Beverton-Holt and Ricker), that assume homogenous distribution of spawners in the simulated river system. Stock-recruit functions most often use two parameters to describe the stock-recruitment relationship. The known values (based on the simulated local parameter values) of total recruitment (R´), S´ (total survival rate) and K´ (total carrying capacity) were then compared to the estimated parameter values based on the assumption of homogenous distribution of spawners in a river. In order to further explore how potential differences in estimated versus known parameter values would be affected by a more realistic scenario, the relative estimation bias (REB) was compared under different theoretical observation error magnitudes (SD=0, 0.2, 0.4 and 0.6).

In **Paper II** the models developed in Paper I were applied to a real-world problem, using model selection criteria to try to identify the underlying spawner behaviour of the Baltic salmon in River Byskeälven (Sweden). In this study, I used long-term empirical data on YOY abundances from electrofishing surveys and the estimated number of spawners from the Baltic salmon stock assessment (ICES, 2023). The local river section characteristics (Ki, S1i and S0) were modelled based on habitat classification of the river, assessed by visual inspections of orthophotos, together with river section area and the distance to the sea. The population dynamics model was fit to the data within a Bayesian statistical framework, applying the different hypotheses about spawner behaviour. Using the widely applicable information criterion (WAIC, Watanabe, 2013), the model fit to the observed data of YOY and spawner abundance was compared among the alternative spawner behaviours, where the lowest WAIC value indicated the model with the best support given the available data.

3.2 Size dependent seaward migration

In **Paper III** we derived an alternative smolt reaction norm based on lengths of parr and smolts in five Swedish rivers (Rickleån, Sävarån, Vindelälven, Testeboån and Mörrumsån). Using this mathematically simple but yet powerful approach, I wanted to explore if only length data from salmon parr and smolts could predict the age distribution of smolts. Moreover, we also evaluated if the method could be used to predict the length and age distribution of smolts in rivers where only parr length data (e.g. electrofishing data) are available. We transferred parameter estimates from the reaction norm in a river where smolt data was available to rivers where only parr length data are available in order to estimate the smolt length frequency and smolt age structure.

Smolt and parr length data were compiled for the study rivers and transformed into length probability density functions using kernel density estimation functions (Parzen, 1962). River-specific smoltification reaction norms were then fitted using nonlinear regression, where parameters: L50% (length at 50% smoltification probability), the slope of the logistic function and the relative growth rate (from parr at the time of electrofishing in the autumn to smolt the following spring) were estimated within the logistic regression model. Based on the length frequency of parr and smolt, we used the same logistic regression model to predict the age distribution of smolts in each river. Predicted smolt age and length distributions were validated by comparing observed frequencies of smolt age and lengths in each of the five rivers. In the next step we evaluated if parameters estimated within the logistic regression from one river could transferred to other rivers in order to predict the smolt length and age distribution based on the parr length measurements. Since the estimated growth parameters might be influenced by the rivers' geographical locations, the influence of latitudinal differences between the rivers was also evaluated based on differences in temperature or photoperiod etc.

3.3 Competition between Baltic salmon (Salmo salar) and trout (Salmo trutta)

In **Paper IV** the competition between Baltic salmon and trout was explored in the initial life stage. Eggs of Baltic salmon (Salmo salar) and brown trout (S. trutta); both originating from river Dalälven were placed in Whitlock-Vibert boxes (Vibert, 1949; Whitlock, 1977) at different densities and species ratios in order to test for density dependent competition. The Whitlock-Vibert boxes where then placed inside 18 competition arenas (Fig.

3). Each competition arena was constantly fed natural water from river Dalälven, providing a steady flow of natural food items. The water velocity was on average 20.9 cm/s. Since habitat heterogeneity affects the competition in salmonids (Finstad et al., 2007; Foldvik et al., 2015), the bottom substrate in this study was standardized using regular golf balls (⌀ = 43 mm). In each arena, one layer of golf balls (n = 320) was placed next to each other, creating equally spaced and sized shelters in all of the competition arenas. The experiment was repeated in three years (2018, 2019 and 2022).

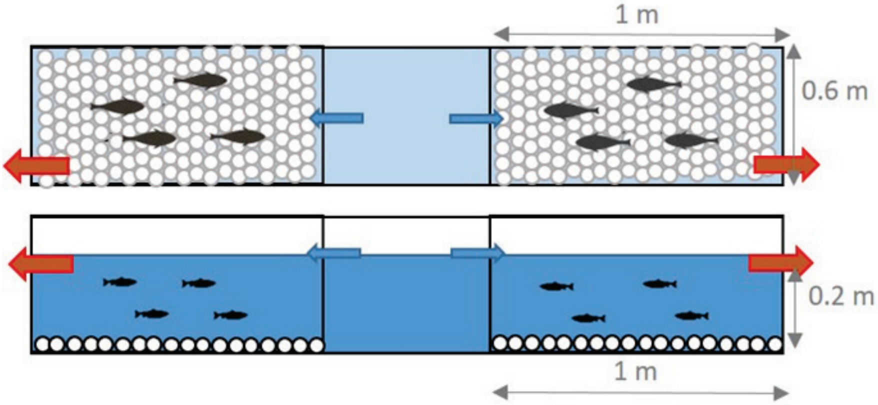


Figure 4. Experimental set-up reproduced from Paper IV. The top illustration shows two experimental arenas from above and the lower illustration shows a side view. In total nine such ‘doubles’ were used, i.e. 18 arenas. Arrows depict water flow (blue=inlet, red=outlet). To simulate habitat heterogeneity, a layer of golf balls was used as a standardized bottom substrate.

Once all eggs had hatched, the fish were left to compete for food and territories for approximately 4 weeks. Weak competitors would escape via the outlet of the competition arena without any possibility to return. When the experiment was terminated, remaining individuals were collected for DNA-based species determination. Genetic analysis was used since visual species determination is almost impossible at that early life-stage. The competitive ability of the two species was statistically analysed using logistic regression, with the response variables being the total number of surviving salmon and the proportion of surviving salmon (in relation to trout) in each competition arena. Predictors were water flow, total number stocked eggs (both salmon and trout), the proportion of salmon stocked and experimental year. From the logistic regressions, predicted survival probabilities were calculated.

4. Results and discussion

4.1 Effects of spawner behaviour in stock-recruitment estimates (Paper I)

The spawner behaviours evaluated affected the stock-recruitment relationship and parameters estimated within the stock-recruitment functions. However, the magnitude of the relative bias in estimated parameters when assuming a Beverton-Holt or Ricker stock-recruitment function depended on the underlying “true” spawner behaviour. When the underlying spawner behaviour was based on the local carrying capacity (hab Q) or IFD, no or negligible bias was introduced. Meanwhile, if the spawner behaviour was random or following a stepwise distribution, the bias was considerably higher. These results were consistent for both a Beverton-Holt and a Ricker stock-recruitment function, and when additional measurement errors were added. The relative estimation bias (REB) and effects on recruitment result mainly from the fact that in some of the spawner behaviours, the local spawning sites are either unused or underutilized. These results suggests that ignoring the underlying spawner behaviour in stock-recruitment analyses can introduce bias when using a two-parameter stock-recruitment function for the whole river. Ultimately this could lead to unsustainable harvest rates if the stock-recruitment relationship if overestimated or loss of yield if the relationship is underestimated.

Under the Beverton-Holt and Ricker models, the spawning individuals are assumed to distribute homogenously in a spawning environment with all offspring suffering the same density-dependent mortality, independent of where they were born. For many fish species, this is not realistic and several alternative spawner behaviours deviating from this assumption have been suggested (Bouchard et al., 2018; Finstad et al., 2013; Haugen et al., 2006; Huntsman and Petty, 2014). The spawner behaviours used in our study are perhaps not realistic either, but the behaviours provide insights into how the deviations from the spawner behaviour assumptions in commonly used stock recruitment models could affect the stock-recruitment relationship. In the future, it would be interesting to also include alternative spawner behaviour models.

Depending on the level of measurement error in observations of recruitment, the relative contribution from the spawner behaviour to the overall bias might be of subordinate concern. At least for the ideal free distribution and habitat quality spawner behaviours. This further emphasizes the importance of reducing or otherwise handling measurement error in the data (Kehler et al., 2002; Walters and Ludwig, 1981).

Our study suggests that including spawner behaviour in stock-assessments is important, and therefore, improved knowledge about the distribution of spawners is warranted. There are methods for identifying the spatial spawning distribution, e.g. telemetry studies (Dean et al., 2014) or nest counts (Finstad et al., 2013), but there is still no general spawner distribution model that can be applied in stock assessments. Earlies studies have showed that individuals might exhibited strong intra-seasonal site fidelity (Lowerre-Barbieri et al., 2013), although individuals also showed some variability in their spatio-temporal behaviour. In addition, Peacock and Holt (2012) made sensitivity analyses indicating that high observation error and straying of spawners may mask changes in distribution, and that by monitoring only sites with high spawner abundance (which is common), result in biased production estimates. Based on these results and the results from **Paper I**, I suggest that spawner behaviours should be defined and included in stock assessments in order to reduce the risk of introducing bias in vital parameter estimates in fisheries management.

4.2 Evaluating alternative spawner distribution models for Atlantic salmon (Paper II)

The model comparison indicated greatest support for the homing behaviour, given the observed data. Homing has previously been suggested to be the underlying spawner behaviour for salmonids (Aas, 2011; Cram et al., 2013; Dittman and Quinn, 1996; Miettinen et al., 2021; Vähä et al., 2007). However, the difference in WAIC between homing and IFD (ΔWAIC) indicates that the IFD distribution might also be a candidate spawner behaviour model. At spawner equilibrium, a strict (100%) homing behaviour would give equal estimates of fitness. However, we allowed a small probability of straying in the homing behaviour, moreover, the spawner abundance in River Byskeälven is most probably not at equilibrium. The results in **Paper II** also provide valuable estimates of the migration mortality per kilometre and estimates of the total carrying capacity in River Byskeälven. However these estimates differed depending on the spawning behaviour. Therefore, this method does not only provide opportunities to evaluate the underlying spawner behaviour of Atlantic salmon in the Baltic Sea, but also valuable estimates of population regulation parameters that are important in stock assessments.

4.3 Growth and smoltification of the Atlantic salmon (Paper III)

In this study, we showed how the length and age distribution at smoltification could be determined from length distributions of parr and smolt. The results indicate that the method produces good predictions of smolt age and size, and that the majority of smolts start migration at a size of 106 mm. This method is applicable to data where only the lengths of the sampled parr and smolt are available, in order to determine the age at smoltification for salmon. Most other smolt reaction norms also include the optimum age for smoltification (Heino et al., 2002). However, optimum age at smoltification could also be derived from the nonlinear regression method we applied, using the probability density for the estimated length classes of parr.

The size at seaward migration in salmon has important implications for the productivity of a stock since it affects the number of years spent at sea (Erkinaro et al., 2019) and thereby fecundity (Thorpe et al., 1984). Thus, information on the size at smoltification could be used in stock-assessments. The method presented in this paper provides a simple and clear but still powerful statistical method that can be used to predict the size and age at smoltification. However, the transferability of parameter estimates from one river to another seemed to be influenced by the geographic proximity. The most southern river (Mörrumsån) generated parameter estimates that did not predict the observed length and age distribution of smolt in the other four rivers (more northerly located) well. The same trend was observed when Mörrumsån parameters were used in order to estimate length and age at smoltification in the four other rivers. This indicates that latitudinal differences are important for the estimated growth from parr to smolt. Thus, the results from Paper III suggest that this difference might be influenced by for example mean annual water temperature. In order to obtain more general estimates of growth, the growth parameter could be modelled as a function of temperature or photoperiod. However, this method could most probably be used in closely located rivers to predict length and age at smoltification.

4.4 Interspecific competition of two closely related species (Paper IV)

The survival rate for Atlantic salmon and brown trout combined across the years and the experimental arenas was 0.047±0.009 (n=36). The proportion of surviving salmon did not depend on water flow or the total number of eggs stocked from both species. There was a positive effect on survival by the proportion of stocked salmon eggs, i.e. the higher proportion of stocked salmon eggs, the higher proportion of salmon survived (pooled correlation: r=0.470; p=0.024, n=24). The relative proportion of salmon among all surviving individuals was 0.937±0.021 in 2018 and 0.139±0.073 in 2022. In other words, in 2018, salmon had a much higher survival rate than brown trout, but in 2022, the result reversed. In 2019, Atlantic salmon had a slightly higher survival rate (0.654±0.193), but not as clear as the effect in 2018.

Thus, this study gave mixed, or contradictory, results. In the first experimental year, Atlantic salmon outcompeted brown trout when occurring simultaneously at the same spot. However, the result from the second year demonstrated brown trout dominance over salmon. In the field, most brown trout hatch, emerge and begin feeding earlier than Atlantic salmon (e.g. Crisp and Ottaway, 1981; Jensen et al., 1989; Lura and Sægrov, 1993) and several studies have showed that water temperature affects the competitive abilities of other fish species (e.g. Watz et al. 2019). In our study, the water temperature during 2022 was on average 1-2 °C higher in comparison to 2018, from mid-March to mid-April. At 10°C the growth rate of a 0.5 g brown trout increases about 2% per day, whereas Atlantic salmon of the same size and at the same temperature have a growth rate of 1.3% per day (Solomon and Lightfoot, 2008). Thus, brown trout may benefit more from higher spring temperatures than Atlantic salmon, since the brown trout fry growth faster and thereby outgrow and outcompete Atlantic salmon fry during warmer springs. During cooler springs, the roles can be reversed. This conclusion is, however, preliminary and rather speculative, and further experiments controlling temperature are warranted to further evaluate the effect from temperature.

The use of different families also could have influenced the survival rates. In our study eggs from 7-9 females of each species were used and some of them in more than one arena. Murray and Beacham (1986), used different stocking densities and families of chum salmon (Oncorhynchus keta) and noted that embryo survival rates were significantly different among families but not between incubation densities. A similar effect could have influenced our results.

In conclusion, my study shows (1) that the number of stocked eggs (i.e. density of hatched fry) did not affect the number of individuals remaining at the hatching area; (2) that the outcome of the competition between Atlantic salmon and brown trout, when hatching at the same time and the same location, might differ significantly between years; and (3) that spring water temperature might be an important factor for the observed results. This, however, needs to be investigated further, using different water temperatures and bottom structures. In addition, as our study only covers three years that differed substantially (in terms of temperature), the study would require further years of data and control of temperature in order to fully evaluate the potential effects of temperature in the competition between salmon and brown trout.

5. Conclusions and future perspectives

In this thesis I have explored how spatial distribution and inter- and intraspecific competition affect population distribution and regulation. I have also developed new methods for determining the spawner distribution behaviour and its consequences on stock-recruit analyses using empirical data and spawner behaviour models. Moreover, I have developed an alternative method for prediction of the body size that determines the timing of smoltification and seaward migration in young salmon. All of these different parts of my thesis have mainly been focusing on Atlantic salmon, but some of the results may also be valuable for other salmonid species and perhaps also other fish species in general.

The spawner behaviour models developed in this thesis were based on potential spawner behaviours common to many fish species. I find that the spawner behaviour can cause bias in vital parameter estimates in stock recruitment functions if the spawner behaviour is ignored. The models evaluated in paper I and paper II can potentially be used within population models and stock-recruitment functions, such as the Beverton-Holt and Ricker, potentially reducing bias in resulting estimates and status evaluations. I also found that if the available stock-recruitment data suffer from observation errors, or do not cover contrasting population abundances, the potential effects of the spawner behaviours might be of subordinate concern. However, this highly depends on the specific spawner behaviour. Therefore, more attention should be given to the spawner behaviour in future studies in order to obtain accurate unbiased estimates of population productivity. The spawner behaviour models can also be used to determine the “real” underlying spawner behaviour, by comparing the fit based on the different spawner behaviour models to empirical data. This finding provides an additional method apart from other already existing migration spatial movement methods, such as telemetry or mark-recapture. The Bayesian framework used herein for simulating the dynamics of an age-structured salmon population could in the future be used for testing additional or perhaps combined spawner behaviour models. Moreover, I developed a method for habitat classification of rivers using remote sensing. This method could also be used in order to determine migration mortality rates and the total carrying capacity of a river. The findings and method development in papers I and II provide a solid platform for future research in the field of spawner behaviour and population regulation.

I have further showed that it is possible to estimate size and length at smoltification using length data from parr and smolt. Moreover, the results from Paper III also show that for rivers sharing the same abiotic factors, it is possible to transfer parameters, estimated in the reaction norm, from data rich rivers (in terms of smolt and parr length measurements) to rivers were only parr length measurements are available in order to predict the smolt length and age distribution. Lastly, I have examined (Paper IV) the competitive relationship between juvenile salmon and trout. In contrast to other studies, I found that trout may be the stronger competitor, whereas salmon can outcompete trout under some conditions. These conditions are suggested to be water temperature, but further experiments including other environmental variables needs to be conducted.

All of the processes studied in this thesis influence the population regulation spawner behaviour models in Atlantic salmon from the Baltic Sea. Spawner behaviours affects the survival rates of recruits based on underutilization of spawning habitats, and if this is not considered in stock assessment this might generate bias in parameter estimates of vital population dynamic parameters. Age and length at smoltification might ultimately influence the post-smolt survival and fecundity, and interspecific competition between salmon and brown trout be temperature dependent.

In summary, this thesis provides insights in some processes regulating populations of the Atlantic salmon, and provide novel methods that can be used to estimate and predict the effects from these processes.

References

Aas, Ø. (Ed.), 2011. Atlantic salmon ecology. Blackwell Pub, Chichester ; Ames, Iowa.

Abrams, P.A., Ginzburg, L.R., 2000. The nature of predation: prey dependent, ratio dependent or neither? Trends Ecol. Evol. 15, 337–341. https://doi.org/10.1016/S0169-5347(00)01908-X

Andersen, K.H., Jacobsen, N.S., Jansen, T., Beyer, J.E., 2017. When in life does density dependence occur in fish populations? Fish Fish 18, 656–667. https://doi.org/10.1111/faf.12195

Andrewartha, H.G., 1957. The Use of Conceptual Models in Population Ecology. Cold Spring Harb Symp Quant Biol 22, 219–236. https://doi.org/10.1101/SQB.1957.022.01.022

Andrewartha, H.G., Birch, L.C., 1954. The Distribution and abundance of animals. University of Chicago Press, Chicago [etc.

Arcese, P., Smith, J.N.M., 1988. Effects of Population Density and Supplemental Food on Reproduction in Song Sparrows. Journal of Animal Ecology 57, 119–136. https://doi.org/10.2307/4768

Bergman, E., Greenberg, L.A., 1994. Competition between a planktivore, a benthivore, and a species with ontogenetic diet shifts. Ecology 75, 1233–1245.

Berryman, A.A., 2004. Limiting Factors and Population Regulation. Oikos 105, 667–670.

Beverton, R.J.H., Holt, S.J., 1957. On the dynamics of exploited fish populations. Fisheries Investigation Series 2, volume 19, UK Ministry of Agriculture. Fisheries, and Food, London, UK.

Bouchard, C., Bardonnet, A., Buoro, M., Tentelier, C., 2018. Effects of spatial aggregation of nests on population recruitment: the case of a small population of Atlantic salmon. Ecosphere 9, e02178. https://doi.org/10.1002/ecs2.2178

Brännström, Å., Sumpter, D.J.T., 2005. The Role of Competition and Clustering in Population Dynamics. Proceedings: Biological Sciences 272, 2065–2072.

Cadrin, S.X., Goethel, D.R., Berger, A., Jardim, E., 2023. Best practices for defining spatial boundaries and spatial structure in stock assessment. Fisheries Research 262, 106650. https://doi.org/10.1016/j.fishres.2023.106650

Case, T.J., Gilpin, M.E., 1974. Interference Competition and Niche Theory. PNAS 71, 3073–3077.

Cherrett, J.M., Bradshaw, A.D. (Eds.), 1989. Ecological concepts: the contribution of ecology to an understanding of the natural world. Blackwell Scientific Publications ; Publishers' Business Service, Oxford [England] ; Boston : Brookline Village, Mass.

Conn, P.B., Williams, E.H., Shertzer, K.W., 2010. When can we reliably estimate the productivity of fish stocks? Can. J. Fish. Aquat. Sci. 67, 511–523. https://doi.org/10.1139/F09-194

Cram, J.M., Torgersen, C.E., Klett, R.S., Pess, G.R., May, D., Pearsons, T.N., Dittman, A.H., 2013. Tradeoffs between homing and habitat quality for spawning site selection by hatchery-origin Chinook salmon. Environ Biol Fish 96, 109–122. https://doi.org/10.1007/s10641-012-0026-1

Crisp, P.A., Ottaway, E.M., 1981. Comparison of observed and predicted dates of eyeing, hatching and swim-up for brown trout and Atlantic salmon.

Dean, M.J., Hoffman, W.S., Zemeckis, D.R., Armstrong, M.P., 2014. Fine-scale diel and gender-based patterns in behaviour of Atlantic cod (Gadus morhua) on a spawning ground in the Western Gulf of Maine. ICES J. Mar. Sci. 71, 1474–1489. https://doi.org/10.1093/icesjms/fsu040

Dittman, A.H., Quinn, T.P., 1996. Homing in Pacific salmon: Mechanisms and ecological basis. J. Exp. Biol. 199, 83–91.

Eikeset, A.M., Dunlop, E.S., Heino, M., Storvik, G., Stenseth, N.C., Dieckmann, U., 2016. Roles of density-dependent growth and life history evolution in accounting for fisheries-induced trait changes. PNAS 113, 15030–15035. https://doi.org/10.1073/pnas.1525749113

Einum, S., Nislow, K.H., Reynolds, J.D., Sutherland, W.J., 2008. Predicting population responses to restoration of breeding habitat in Atlantic salmon. Journal of Applied Ecology 45, 930–938. https://doi.org/10.1111/j.1365-2664.2008.01464.x

Einum, S., Robertsen, G., Nislow, K.H., McKelvey, S., Armstrong, J.D., 2011. The spatial scale of density-dependent growth and implications for dispersal from nests in juvenile Atlantic salmon. Oecologia 165, 959–969. https://doi.org/10.1007/s00442-010-1794-y

Einum, S., Sundt-Hansen, L., Nislow, K.H., 2006. The Partitioning of Density-Dependent Dispersal, Growth and Survival throughout Ontogeny in a Highly Fecund Organism. Oikos 113, 489–496.

Erkinaro, J., Czorlich, Y., Orell, P., Kuusela, J., Falkegård, M., Länsman, M., Pulkkinen, H., Primmer, C.R., Niemelä, E., 2019. Life history variation across four decades in a diverse population complex of Atlantic salmon in a large subarctic river. Can. J. Fish. Aquat. Sci. 76, 42–55. https://doi.org/10.1139/cjfas-2017-0343

Fernández-Bellon, D., Cortés-Avizanda, A., Arenas, R., Donázar, J.A., 2016. Density-dependent productivity in a colonial vulture at two spatial scales. Ecology 97, 406–416. https://doi.org/10.1890/15-0357.1

Finstad, A.G., Einum, S., Forseth, T., Ugedal, O., 2007. Shelter availability affects behaviour, size-dependent and mean growth of juvenile Atlantic salmon. Freshwater Biology 52, 1710–1718. https://doi.org/10.1111/j.1365-2427.2007.01799.x

Finstad, A.G., Sættem, L.M., Einum, S., 2013. Historical abundance and spatial distributions of spawners determine juvenile habitat accessibility in salmon: implications for population dynamics and management targets. Can. J. Fish. Aquat. Sci. 70, 1339–1345. https://doi.org/10.1139/cjfas-2012-0455

Foldvik, A., Einum, S., Finstad, A.G., Ugedal, O., 2015. Linking watershed and microhabitat characteristics: effects on production of Atlantic salmonids (Salmo salar and Salmo trutta). Ecology of Freshwater Fish 26, 260–270. https://doi.org/10.1111/eff.12272

Ford, J.R., Swearer, S.E., 2013. Two's company, three's a crowd: Food and shelter limitation outweigh the benefits of group living in a shoaling fish. Ecology 94, 1069–1077.

Fretwell, S.D., Lucas, H.L., 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. Acta Biotheor 19, 16–36. https://doi.org/10.1007/BF01601953

Friedland, K.D., Haas, R.E., 1996. Marine post-smolt growth and age at maturity of Atlantic salmon. Journal of Fish Biology 48, 1–15. https://doi.org/10.1111/j.1095-8649.1996.tb01414.x

Gamelon, M., Vriend, S.J.G., Engen, S., Adriaensen, F., Dhondt, A.A., Evans, S.R., Matthysen, E., Sheldon, B.C., Sæther, B.-E., 2019. Accounting for interspecific competition and age structure in demographic analyses of density dependence improves predictions of fluctuations in population size. Ecology Letters 22, 797–806. https://doi.org/10.1111/ele.13237

Gilbert, D.J., 1997. Towards a new recruitment paradigm for fish stocks. Can. J. Fish. Aquat. Sci. 54, 969–977. https://doi.org/10.1139/f96-272

Haddon, M., 2001. Modelling and quantitative methods in fisheries. Chapman & Hall/CRC, Boca Raton, Fla.

Hasegawa, K., 2016. The density dependent interspecific competition between nonnative salmonids, rainbow trout and brown trout. Environ Biol Fish 99, 433–438. https://doi.org/10.1007/s10641-016-0484-y

Haugen, T.O., Winfield, I.J., Vøllestad, L.A., Fletcher, J.M., James, J.B., Stenseth, N.Chr., 2006. The Ideal Free Pike: 50 Years of Fitness-Maximizing Dispersal in Windermere. Proceedings: Biological Sciences 273, 2917–2924.

Heino, M., Dieckmann, U., GODø, O.R., 2002. Measuring Probabilistic Reaction Norms for Age and Size at Maturation. Evolution 56, 669–678. https://doi.org/10.1111/j.0014-3820.2002.tb01378.x

Hilborn, R., Fulton, E.A., Green, B.S., Hartmann, K., Tracey, S.R., Watson, R.A., 2015. When is a fishery sustainable? Can. J. Fish. Aquat. Sci. 72, 1433–1441. https://doi.org/10.1139/cjfas-2015-0062

Hixon, M.A., Anderson, T.W., Buch, K.L., Johnson, D.W., McLeod, J.B., Stallings, C.D., 2012. Density dependence and population regulation in marine fish: a large-scale, long-term field manipulation. Ecological Monographs 82, 467–489. https://doi.org/10.1890/11-1525.1

Hixon, M.A., Pacala, S.W., Sandin, S.A., 2002. Population Regulation: Historical Context and Contemporary Challenges of Open vs. Closed Systems. Ecology 83, 1490–1508. https://doi.org/10.2307/3071969

Honěk, A., 1993. Intraspecific Variation in Body Size and Fecundity in Insects: A General Relationship. Oikos 66, 483–492. https://doi.org/10.2307/3544943

Honeyfield, D.C., Brown, S.B., Fitzsimons, J.D., Tillitt, D.E., 2005. Early Mortality Syndrome in Great Lakes Salmonines. J Aqua Anim Hlth 17, 1–3. https://doi.org/10.1577/H04-012.1

Hulson, P.-J., Hanselman, D., Quinn, T., 2011. Effects of process and observation errors on effective sample size of fishery and survey age and length composition using variance ratio and likelihood methods. ICES Journal of Marine Science 68, 1548–1557. https://doi.org/10.1093/icesjms/fsr102

Huntsman, B.M., Petty, J.T., 2014. Density-Dependent Regulation of Brook Trout Population Dynamics along a Core-Periphery Distribution Gradient in a Central Appalachian Watershed. PLoS One 9. https://doi.org/10.1371/journal.pone.0091673

ICES, 2023. Baltic Salmon and Trout Assessment Working Group (WGBAST). ICES Scientific Reports. https://doi.org/10.17895/ICES.PUB.22800983.V3

ICES, 2019. Baltic Salmon and Trout Assessment Working Group. https://doi.org/10.17895/ices.pub.4979

Imre, I., Grant, J.W.A., Cunjak, R.A., 2005. Density-dependent growth of young-of-the-year Atlantic salmon Salmo salar in Catamaran Brook, New Brunswick. Journal of Animal Ecology 74, 508–516. https://doi.org/10.1111/j.1365-2656.2005.00949.x

Imsland, A.K., Handeland, S.O., Stefansson, S.O., 2014. Photoperiod and temperature effects on growth and maturation of pre- and post-smolt Atlantic salmon. Aquacult Int 22, 1331–1345. https://doi.org/10.1007/s10499-014-9750-1

Jensen, A.J., Johnsen, B.O., Saksgård, L., 1989. Temperature requirements in Atlantic salmon (Salmo salar), brown trout (Salmo trutta), and Arctic char (Salvelinus alpinus) from hatching to initial feeding compared with geographic distribution. Canadian Journal of Fisheries and Aquatic Sciences 46, 786–789.

Jonsson, N., Jonsson, B., Hansen, L.P., 1998. The relative role of density-dependent and density-independent survival in the life cycle of Atlantic salmon Salmo salar. Journal of Animal Ecology 67, 751–762. https://doi.org/10.1046/j.1365-2656.1998.00237.x

Jutila, E., Jokikokko, E., Julkunen, M., 2006. Long-term changes in the smolt size and age of Atlantic salmon, Salmo salar L., in a northern Baltic river related to parr density, growth opportunity and postsmolt survival. Ecology of Freshwater Fish 15, 321–330. https://doi.org/10.1111/j.1600-0633.2006.00171.x

Kareiva, P., Mullen, A., Southwood, R., 1990. Population Dynamics in Spatially Complex Environments: Theory and Data [and Discussion]. Philosophical Transactions: Biological Sciences 330, 175–190.

Kehler, D.G., Myers, R.A., Field, C.A., 2002. Measurement error and bias in the maximum reproductive rate for the Ricker model. Can. J. Fish. Aquat. Sci. 59, 854–864. https://doi.org/10.1139/f02-060

Koljonen, M.-L., 2001. Conservation goals and fisheries management units for Atlantic salmon in the Baltic Sea area. Journal of Fish Biology 59, 269–288. https://doi.org/10.1111/j.1095-8649.2001.tb01390.x

Letcher, B.H., Gries, G., Juanes, F., 2002. Survival of Stream-Dwelling Atlantic Salmon: Effects of Life History Variation, Season, and Age. Transactions of the American Fisheries Society 131, 838–854. https://doi.org/10.1577/1548-8659(2002)131<0838:SOSDAS>2.0.CO;2

Linton, B.C., Bence, J.R., 2008. Evaluating methods for estimating process and observation error variances in statistical catch-at-age analysis. Fisheries Research 94, 26–35. https://doi.org/10.1016/j.fishres.2008.06.014

Lorenzen, K., 2008. Fish population regulation beyond "stock and recruitment": The role of density-dependent growth in the recruited stock. Bull. Mar. Sci. 83, 181–196.

Lowerre-Barbieri, S.K., Walters, S., Bickford, J., Cooper, W., Muller, R., 2013. Site fidelity and reproductive timing at a spotted seatrout spawning aggregation site: individual versus population scale behavior. Marine Ecology Progress Series 481, 181–197.

Lura, H., Sægrov, H., 1993. Timing of spawning in cultured and wild Atlantic salmon (Salmo salar) and brown trout (Salmo trutta) in the River Vosso, Norway. Ecology of Freshwater Fish 2, 167–172.

Malthus, T.R., 1798. An Essay on the Principle of Population, as it Affects the Future Imporvement of Society, with Remarks on the Speculations of Mr. Godwin, M. Condorcet, and Other Writers. The Lawbook Exchange, Ltd.

Marshall, C.T., Needle, C.L., Thorsen, A., Kjesbu, O.S., Yaragina, N.A., 2006. Systematic bias in estimates of reproductive potential of an Atlantic cod (Gadus morhua) stock: implications for stock–recruit theory and management. Can. J. Fish. Aquat. Sci. 63, 980–994. https://doi.org/10.1139/f05-270

Miettinen, A., Palm, S., Dannewitz, J., Lind, E., Primmer, C.R., Romakkaniemi, A., Östergren, J., Pritchard, V.L., 2021. A large wild salmon stock shows genetic and life history differentiation within, but not between, rivers. Conserv Genet. https://doi.org/10.1007/s10592-020-01317-y

Milne, A., 1962. On a theory of natural control of insect population. Journal of Theoretical Biology 3, 19–50. https://doi.org/10.1016/S0022-5193(62)80003-4

Montorio, L., Evanno, G., Nevoux, M., 2018. Intra- and interspecific densities shape life-history traits in a salmonid population. Oecologia 188, 451–464. https://doi.org/10.1007/s00442-018-4213-4

Morris, D.W., 2003. Toward an Ecological Synthesis: A Case for Habitat Selection. Oecologia 136, 1–13.

Murdoch, W.W., 1994. Population regulation in theory and practice. Ecology 75, 271–287.

Murray, B.G., 1999. Can the Population Regulation Controversy Be Buried and Forgotten? Oikos 84, 148–152. https://doi.org/10.2307/3546875

Murray, C.B., Beacham, T.D., 1986. Effect of incubation density and substrate on the development of chum salmon eggs and alevins. The Progressive Fish-Culturist 48, 242–249.

Myers, R.A., Bowen, K.G., Barrowman, N.J., 1999. Maximum reproductive rate of fish at low population sizes. Can. J. Fish. Aquat. Sci. 56, 2404–2419. https://doi.org/10.1139/f99-201

Needle, C.L., 2002. Recruitment models: diagnosis and prognosis. Reviews in Fish Biology and Fisheries 11, 95–111. https://doi.org/10.1023/A:1015208017674

Palmé, A., Wennerström, L., Guban, P., Ryman, N., Laikre, L., 2012. Compromising Baltic salmon genetic diversity: conservation genetic risks associated with compensatory releases of salmon in the Baltic Sea.

Parzen, E., 1962. On estimation of a probability density function and mode. The annals of mathematical statistics 33, 1065–1076.

Peacock, S.J., Holt, C.A., 2012. Metrics and sampling designs for detecting trends in the distribution of spawning Pacific salmon (Oncorhynchus spp.). Can. J. Fish. Aquat. Sci. 69, 681–694. https://doi.org/10.1139/f2012-004

Persson, L., Raunsgard, A., Thorstad, E.B., Østborg, G., Urdal, K., Sægrov, H., Ugedal, O., Hindar, K., Karlsson, S., Fiske, P., Bolstad, G.H., 2023. Iteroparity and its contribution to life-history variation in Atlantic salmon. Can. J. Fish. Aquat. Sci. 80, 577–592. https://doi.org/10.1139/cjfas-2022-0126

Pulkkinen, H., Mäntyniemi, S., 2013. Maximum survival of eggs as the key parameter of stock–recruit meta-analysis: accounting for parameter and structural uncertainty. Can. J. Fish. Aquat. Sci. 70, 527–533. https://doi.org/10.1139/cjfas-2012-0268

Pulliam, H.R., 1988. Sources, sinks, and population regulation. The American Naturalist 132, 652–661.

Quinn, T.J., Deriso, R.B., 1999. Quantitative fish dynamics, Biological resource management series. Oxford University Press, New York.

Reddingius, J., den Boer, P.J., 1970. Simulation Experiments Illustrating Stabilization of Animal Numbers by Spreading of Risk. Oecologia 5, 240–284.

Relyea, R., 2021. Ecology: the economy of nature, Ninth edition. ed. macmillan international, higher education, New York.

Ricker, W.E., 1975. Computation and interpretation of biological statistics of fish populations. Bulletin of the Fisheries Research Board of Canada 191, 1–382.

Rose, K.A., Cowan, J.H., Winemiller, K.O., Myers, R.A., Hilborn, R., 2001. Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. Fish and Fisheries 2, 293–327. https://doi.org/10.1046/j.1467-2960.2001.00056.x

Säisä, M., Koljonen, M.-L., Gross, R., Nilsson, J., Tähtinen, J., Koskiniemi, J., Vasemägi, A., 2005. Population genetic structure and postglacial colonization of Atlantic salmon (Salmo salar) in the Baltic Sea area based on microsatellite DNA variation. Can. J. Fish. Aquat. Sci. 62, 1887–1904. https://doi.org/10.1139/f05-094

Sakuramoto, K., 2005. Does the Ricker or Beverton and Holt type of stock-recruitment relationship truly exist? Fish Sci 71, 577–592. https://doi.org/10.1111/j.1444-2906.2005.01002.x

Sibly, R.M., Hone, J., 2002. Population Growth Rate and Its Determinants: An Overview. Philosophical Transactions: Biological Sciences 357, 1153–1170.

Sinclair, A.R.E., Pech, R.P., 1996. Density Dependence, Stochasticity, Compensation and Predator Regulation. Oikos 75, 164–173. https://doi.org/10.2307/3546240

Svanbäck, R., Bolnick, D.I., 2007. Intraspecific competition drives increased resource use diversity within a natural population. Proceedings of the Royal Society B: Biological Sciences 274, 839–844.

Thorpe, J.E., Miles, M.S., Keay, D.S., 1984. Developmental rate, fecundity and egg size in Atlantic salmon, Salmo salar L. Aquaculture 43, 289–305.

Thunell, V., Gårdmark, A., Huss, M., Vindenes, Y., 2022. Optimal energy allocation trade-off driven by size-dependent physiological and demographic responses to warming. Ecology e3967.

Turchin, P., 2003. Complex population dynamics: a theoretical/empirical synthesis, Monographs in population biology. Princeton University Press, Princeton, N.J.

Turchin, P., 1999. Population regulation: a synthetic view. Oikos 153–159.

Turchin, P., 1995. Population Regulation: Old Arguments and a New Synthesis, in: Cappuccino, N., Price, P.W. (Eds.), Population Dynamics. Academic Press, San Diego, pp. 19–40. https://doi.org/10.1016/B978-012159270-7/50003-8

Vähä, J.-P., Erkinaro, J., Niemelä, E., Primmer, C.R., 2007. Life-history and habitat features influence the within-river genetic structure of Atlantic salmon. Molecular Ecology 16, 2638–2654. https://doi.org/10.1111/j.1365-294X.2007.03329.x

Verhulst, P.-F., 1838. Notice sur la loi que la population suit dans son accroissement. correspondance mathématique et physique publiée par a. Quetelet 10, 113–121.

Vert-pre, K.A., Amoroso, R.O., Jensen, O.P., Hilborn, R., 2013. Frequency and intensity of productivity regime shifts in marine fish stocks. Proceedings of the National Academy of Sciences 110, 1779–1784.

Vibert, R., 1949. Du repeuplement en truites et saumons par enfouissement de" boîtes d'alevinage" garnies d'oeufs dans les graviers. Bulletin francais de Pisciculture 125–150.

Vincenzi, S., Satterthwaite, W.H., Mangel, M., 2012. Spatial and temporal scale of density-dependent body growth and its implications for recruitment, population dynamics and management of stream-dwelling salmonid populations. Rev Fish Biol Fisheries 22, 813–825. https://doi.org/10.1007/s11160-011-9247-1

Walters, C.J., 1985. Bias in the estimation of functional relationships from time series data. Canadian Journal of Fisheries and Aquatic Sciences 42, 147–149.

Walters, C.J., Ludwig, D., 1981. Effects of Measurement Errors on the Assessment of Stock–Recruitment Relationships. Can. J. Fish. Aquat. Sci. 38, 704–710. https://doi.org/10.1139/f81-093

Walters, C.J., Martell, S.J.D., 2004. Fisheries ecology and management. Princeton University Press, Princeton, N.J.

Watanabe, S., 2013. A widely applicable Bayesian information criterion. The Journal of Machine Learning Research 14, 867–897.

Watz, J., Otsuki, Y., Nagatsuka, K., Hasegawa, K., Koizumi, I., 2019. Temperature-dependent competition between juvenile salmonids in small streams. Freshwater Biology 64, 1534–1541.

Whitlock, D., 1977. The Whitlock vibert box handbook. Federation of Fly Fishermen.

Zimmermann, F., Enberg, K., Mangel, M., 2021. Density-independent mortality at early life stages increases the probability of overlooking an underlying stock–recruitment relationship. ICES Journal of Marine Science 78, 2193–2203. https://doi.org/10.1093/icesjms/fsaa246

Popular science summary

When harvesting natural populations, we need to make sure that the harvest rates are sustainable. If natural populations are overexploited, we risk losing populations and vital ecosystem functions. In order to achieve sustainable harvest rates we need to assess and manage populations. This assessment of populations needs to be based on the best possible knowledge of vital population regulatory processes. There are numerous ways that populations can be regulated. These processes can roughly be divided into density-independent (e.g. fishing or weather) or density-dependent (e.g. competition between conspecifics) processes. If we for example harvest a population (density-independent process), we also need to know what other density-dependent processes that affects the mortality in that population in order to not eradicate the population. Most populations are self-regulatory, meaning that the system in which they live can only support a certain number of individuals. At a specific level, the density-dependent competition over common resources will hinder the population from increase in abundance. This means that at some level of abundance the population is producing more individuals than is needed to sustain the population abundance. This further means that if we harvest just this surplus production the population should not decrease in abundance. This is the foundation of fisheries ecology.

Fishing is one of the few activities where we have a commercial outtake from natural populations. In fisheries ecology, the status and development of the harvested populations should be continuously monitored, in order to follow their status. This is performed by the collection of data that is later used in different statistical models. Even if we have profound knowledge of regulatory processes, populations still declines. Therefore, we need not gain more understanding and incorporate regulatory mechanisms in the stock assessment in order to succeed in our management goals.

In this thesis, I evaluate unknown processes and potential sources of bias or in population assessments. More specifically, I evaluate if and how the distribution behaviour of reproducing fish (spawners) might affect the survival of their offspring. By simulate a fish population with different spawner behaviours I found that, depending on the specific behaviour, the distribution of the spawners could affect estimates of the population production. However, if we have many errors in our data from the observations, this problem might be more profound than the spawner behaviour. In the second paper, I investigated if we can use the spawner behaviour models to gain understanding in how spawners of Atlantic salmon in the Baltic Sea actually distribute in nature. By comparing the theoretical behaviour models with what we observe, I found that this method could work for detecting the spawner behaviour. Moreover, based on this method we would also gain important information of population regulatory processes based on the spawner behaviour, which could generate better stock assessments for salmon and other fish species. In my third paper, I tested an alternative method that can be used to estimate at what length and age a juvenile salmon will smoltify and migrate to the sea. This estimation process is not new, but our method provides the possibility to use predictions from one river on another river were data of smolt lengths are missing. This means that we can receive better estimates of the smoltification process, which ultimately could influence the population regulation. In the last paper, I explored how salmon and trout, two closely related fish species, compete during the earliest life stage. Earlier it has been shown that trout is the strongest competitor, but in our experiments, we found that salmon may outcompete trout under certain circumstances and that this pattern may be temperature dependent. From these four studies, I have provided new information and methods for the assessment of harvested fish populations, information that potentially can improve our possibilities to achieve sustainable fisheries.

Populärvetenskaplig sammanfattning

När vi exploaterar naturliga populationer måste vi även försäkra oss om att detta sker på ett hållbart vis. Överexploaterar vi populationer riskerar vi att förlora dessa samt potentiellt vitala ekosystemfunktioner. För att vi ska uppnå ett hållbart nyttjande behöver vi övervaka och förvalta dessa populationer. Denna förvaltning bör alltid grundas i den bästa rådande kunskapen om vitala populationsreglerande processer. Det finns många sätt som en population regleras på. Dessa processer kan delas in i täthetsoberoende- (t.ex. fiske) eller täthetsberoende- (t.ex. konkurrens mellan artfränder). Om vi till exempel exploaterar en population (täthetsoberoende process) måste vi även veta vilka andra täthetsberoende processer som påverkar dödligheten i populationen, för att undvika att populationen inte minskar i abundans. De flesta populationer är självreglerande, vilket betyder att det i ekosystemet endast finns resurser eller plats som räcker till för ett specifikt antal individer. Vid en specifik populationsmängd kommer konkurrensen om gemensamma resurser att hindra populationstillväxten. Det betyder att vid vissa tätheter producerar populationen fler individer än vad som behövs för att upprätthålla en konstant populationsnivå. Det betyder i sin tur att om vi bara nyttjar detta överskott av individer kommer väntas inte populationen att minska på sikt. Detta utgör ett av fiskeriekologins fundament.

Kommersiellt fiske är en av de få aktiviteter där människan bedriver ett kommersiellt uttag från naturliga populationer. I fiskeriekologi bedöms statusen och utvecklingen av de fiskbestånd som fiskas kontinuerligt. Detta görs genom insamlande av data som sedan används i olika statistiska modeller där populationsstatusen skattas. Även om vi har en ökad kännedom om populationsreglerande processer så minskar många fiskpopulationer.

Därför behöver vi mer kunskap om populationsreglering för att uppnå våra förvaltningsmål.
I denna avhandling utvärderar jag olika källor till populationsreglering som antingen är påverkade av bias eller som är okända i populationsförvaltningen. Mer specifikt utvärderar jag om och i så fall hur spridningsbeteendet hos reproducerande fiskar (lekfisk) påverkar överlevnaden hos avkomman. Genom att simulera en fiskpopulation med olika spridningsmönster hos lekfisken, kunde jag konstatera att estimat av populationsproduktionen påverkades av lekfiskens spridningsmönster. Men om vi har stora mätfel i insamlad data så kommer denna effekt vara större än effekten av spridningsmönstret hos lekfisk har. I det andra manuskriptet i avhandlingen så undersökte jag om det går att använda dessa spridningsmönster-modeller för att ta reda på vilket underliggande spridningsmönster som förekommer i en naturlig population av östersjölax. Genom att jämföra hur väl olika spridningsmönster passade med observerade data kom jag fram till att denna vår metod kan användas för att detektera det naturliga spridningsmönstret hos lax i Byskeälven, och att beteendet följde ett homing-beteende (d.v.s. att fisken i hög grad återvänder till födelseplatsen för lek). I mitt tredje manuskript testade jag en alternativ metod för att skatta vid vilken längd och ålder som lax migrerar från älvar till havet. Resultaten från denna studie visar att metoden fungerar väl för att förutse vid vilken längd och ålder som en lax smoltifierar. Parametrarna som estimerades i denna studie kunde även överföras till närliggande älvar för att beräkna vid vilken ålder och storlek som laxen vandrar ut i havet, bara genom att använda data från yngre fiskar (stirr). I det sista manuskriptet i avhandlingen utforskade jag hur konkurrensen mellan yngel av lax och öring ser ut. Tidigare studier har visat att öringen oftast är den starkaste konkurrenten av de två arterna, men våra experiment visar att vi vissa förhållanden så kan laxen konkurrera ut öringen. Vi tror att detta är beroende av temperatur. Med dessa fyra studier så har jag bidragit med mer kunskap för bedömningen av exploaterade fiskpopulationer, kunskap som potentiellt kan förbättra våra möjligheter att uppnå ett hållbart fiske.

Acknowledgements

These doctoral years have been a journey to say the least. A journey that would have been nearly impossible without the support from the people around me. I would therefore like to thank the following for all support and help:

Erik Petersson, my main supervisor and extra dad, who has always been there no matter what. You have supported me with your expertise and wisdom and always asked how the kids are before asking me anything.

Rebecca Whitlock, my co-supervisor and Bayesian sensei. Thank you for putting up with my last minute issues and for introducing me to the pure path of statistics.

Kjell Leonardsson, my co-supervisor and private mathematician. Thank you for always solving stuff and for working night-hours.

Stefan Palm, my co-supervisor and Salmon master. Thank you for your humble feedback on numerous drafts and for informal chats about salmon.

Katarina Magnusson, my co-supervisor. Thank you for all the help and for always being so nice and encouraging. You really made me feel ok when times were dark.

Viktor, Max(imillian), Philip, Erik, Monica, Yvette, Isa, Hege, Alessandro, Renee, Nataliia, Astrid, Duncan, Will, Ben, Olivia and **Yao,** the PhD-gang. Thank you for all the laughs and for all the good times. If I pass today, I will miss being a part of the group. If I do not – see you at the next PhD happening. Also, thank you for always letting me decide stuff so I get things the way I want. Without you guys, the PhD-time would have been so dull.

Viktor T. my academic doppelgänger, and old friend, thanks for all fun and non-fun times we have shared, and for all inspiration. And thank you for always supporting when times are tuff.

People at Sölab, colleagues and friends. Thanks for being so nice and welcoming, and a special thanks to the floorball teammates for always letting me win.

Josefin Sundin, colleague and friend. Thank you for your inspiration and fun conversations. Also thank you for my first publication, but no thanks for your crappy music taste.

Jörgen Rask, Yvonne Ottosson, Elsie-Marie Jansson, Lena Lindersson and **Ann Britt Florin,** Thank you for all your help during my experiments in Älvkarleby. Also thank you for making me not develop "lappsjuka" when staying in Älvkarleby. Your welcoming atmosphere will not be forgotten. I will perhaps not miss the experimental room but I will definitely miss you!

I would also like to thank people outside the academic sphere since without you I would not have been the person I am today for several reasons, so thanks to:

Elsy and **Thomas**, from the first time we met you have treated me as your own son. Thank you for your generosity and support.

Karl, Valentina, Kristina, Johannes, Lisa, Peter, Maria and **Fredrik**¸ my extra family. Thanks for everything, from late night gaming to travel memories, and for being parents to the very best: **Matilda, Elsa, Arvid, Evald, Arthur, IdaKarin, John, Anna, Axel, Olof and Hanna.**

Also thanks to my real family: **Björn, Maria, Håkan, Anneli, Madeleine, Johan, Håkan, Peter, Ida, Andreas, Sanna** and **Fredrik,** for all your support and for you lovely kids: **Gustav, Anton, Jeremias, Amelia, William, Tilda, Ella, Nellie, Alicia, Lukas, Vidar, Astrid, Saga, Harry** and **Luna.**

Jeanette, thank you for always being supportive. Wish you were here.

My dad, thank you for always supporting me in any of my decisions, and for raising my younger brothers and me all by yourself. I do not think you have ever heard it from me, but… I love you!

Sylvia, thanks for all your tricky questions regarding everything and for your patience for all the times you have had to hear me saying "jag ska bara" or "kanske senare" the last couple of years. **Lars**, thank you for always understanding and for being extremely interested in ecological and environmental issues. Thank you **Harald** for always making me smile and for all your crazy antics, and for your lovely songs.

Lena, what would life have been without you? There is so much I would like to say to you but written words will come out short and I rather say them to you in person. People that have not spent considerable (still not enough) time with someone that is regarded as perfect, would never understand our relationship. Thank you for always being there and for everything we have shared so far. Also thank you for being my best friend and the best mother to our kids. I want to grow old with you. I love you!

Received: 22 February 2022 | Revised: 30 November 2022 | Accepted: 9 December 2022
DOI: 10.1002/ece3.9679

Ecology and Evolution Open Access WILEY

RESEARCH ARTICLE

From spawner habitat selection to stock-recruitment: Implications for assessment

Stefan Skoglund[1] | **Rebecca Whitlock**[1] | **Erik Petersson**[1] | **Stefan Palm**[1] | **Kjell Leonardsson**[2]

[1]Department of Aquatic Resources, Institute of Freshwater Research, Swedish University of Agricultural Sciences, Drottningholm, Sweden

[2]Department of Wildlife, Fish and Environmental Studies, Swedish University of Agricultural Sciences, Umeå, Sweden

Correspondence
Stefan Skoglund, Department of Aquatic Resources, Institute of Freshwater Research, Swedish University of Agricultural Sciences, Drottningholm, SE-178 93, Sweden.
Email: stefan.skoglund@slu.se

Funding information
Swedish University of Agricultural Sciences

Abstract

The relationship between the spawning stock size and subsequent number of recruits is a central concept in fisheries ecology. The influence of habitat selection of spawning individuals on the stock-recruitment relationship is poorly known. Here we explore how each of four different spawner behaviors might influence the stock-recruitment relationship and estimates of its parameters in the two most commonly used stock-recruitment functions (Beverton-Holt and Ricker). Using simulated stock-recruitment data generated by four different spawner behaviors applied to multiple discrete habitats, we show that when spawners were distributed proportionally to local carrying capacities, there was small or no bias in estimated recruitment and stock-recruitment parameters. For an ideal free distribution of spawners, larger bias in the estimates of recruitment and stock-recruitment parameters was obtained, whereas a random and a stepwise spawner behavior introduced the largest bias. Using stock-recruitment data corresponding to a "realistic" range of population densities and adding measurement error (20%–60%) to the simulated stock-recruitment data generated larger variation in the estimation bias than what was introduced by the spawner behavior. Thus, for exploited stocks at low population density and where spawning stock size and recruitment cannot be observed perfectly, partial observation of the possible spawner abundance range and measurement error might be of higher concern for management.

KEYWORDS
behavior biology, fisheries management, habitat selection, population ecology, population productivity, stock-recruitment

TAXONOMY CLASSIFICATION
Applied ecology, Behavioural ecology, Conservation ecology, Population ecology, Spatial ecology

1 | INTRODUCTION

Maximizing long-term yield is a common target for the management of exploited fish populations around the world (Hilborn et al., 2015; Vert-pre et al., 2013). The rate of harvest that maximizes yield strongly depends on a population's productivity (potential rate of net population increase), of which the maximum per capita recruitment at low population density (i.e. the slope at the origin of the stock-recruit curve) is a key determinant (Beverton & Holt, 1957; Myers, 2001; Myers & Barrowman, 1996; Quinn & Deriso, 1999; Ricker, 1954). The productivity of an exploited population (stock), thus underlies its response to exploitation, and the level of harvest that it can sustain over the long term (Conn et al., 2010).

Stock-recruitment (SR) models are widely applied in fisheries stock assessments to describe the expected average number of recruits as a function of spawning stock metrics (e.g. eggs or spawning stock biomass). The two most common SR models used in stock assessments are the Beverton-Holt (Beverton & Holt, 1957) and the Ricker (Ricker, 1954) models. These two SR models have different functional forms, where recruitment increases asymptotically with increasing spawning output in a Beverton-Holt model, whereas a Ricker model describes recruitment as a skewed dome-shaped function of spawning output. Both models include parameters that are based on biological density-dependent and -independent processes influencing the productivity of a population. As an example; the slope at the origin of the fitted curve in a SR model can be interpreted as the density-independent maximum reproductive rate, whereas the asymptote (Beverton-Holt model) or the maximum recruitment (Ricker model) describes density-dependent population processes related to the system's carrying capacity (Myers, 2001). The shape of the SR relationship for a specific population correlates to both the evolved life history traits and the reproductive behavior (Foss-Grant et al., 2016), where different stages in the pre-recruited phase can be both density-dependent and -independent (Brooks & Powers, 2007; Taylor et al., 2013).

Stock-recruitment relationships form the basis for reference points (e.g. Maximum sustainable yield, MSY) that are commonly used to evaluate stock-status and specify appropriate catch levels (Haddon, 2001). Thus, obtaining unbiased estimates of such parameters is crucial to avoiding loss of yield and/or unsustainable harvest rates in exploited natural populations (Needle, 2002). Ideally, estimated SR parameters should provide unbiased information on the productivity of a stock (Lee et al., 2012). However, fitting statistical functions to SRdata provides no insight into the biological mechanisms generating the observed patterns.

Estimated SR relationships are often uncertain and/or biased (Conn et al., 2010). A variety of factors influencing SR estimates has been suggested, e.g. time-series bias (Walters, 1985), observation (Walters & Ludwig, 1981), and process errors (Linton & Bence, 2008), productivity regimes (Gilbert, 1997; Vert-pre et al., 2013), and non-stationary dynamics (Feiner et al., 2015; Quinn & Deriso, 1999). Biological and ecological aspects such as age structure, spatial distribution, fecundity and spawning patterns are also known to influence the variation in recruitment (Green, 2008; Shelton et al., 2012). However, it remains poorly understood if (and how) the spatial distribution of spawning individuals may generate potential bias in SR estimates, although such behavioral patterns among spawners have long been acknowledged as a key factor affecting population productivity and regulation (Fretwell & Lucas, 1970; Jonzen et al., 2004; Morris, 1987; Pulliam & Danielson, 1991).

In fisheries applications, traditional SR models typically assume that the parameters determining productivity are constant across the range of reproductive output (Holt & Michielsens, 2020). For fish that spawn over large areas, this either that productivity is the same over the whole environment, or if it varies, that spawners distribute themselves in homogenously in the spawning environment. For many fish species, however, reproductive environments and the selection of habitats for reproduction among adults are known to deviate from these simplified assumptions (Bietz, 1981; Dingsør et al., 2007; Falcy, 2015; Finstad et al., 2013; Haugen et al., 2006; Purchase & Hutchings, 2008; Skjæraasen et al., 2011). Such deviations are expected to directly influence the initial intraspecific competition experienced by the offspring if the juvenile life-stages are less mobile than the adults (as in many fish species). This may, in turn, ultimately influence population regulation if density dependence acts strongest in the initial life-stages (Einum, Nislow, et al., 2008; Sinclair & Pech, 1996; Teichert et al., 2010; Turchin, 1999). As an example, for Atlantic salmon (*Salmo salar*), an anadromous species with heterogeneously distributed spawning aggregations in freshwater river habitats (Finstad et al., 2013; Fleming, 1996), it has been shown that juvenile survival is negatively correlated with egg density (Einum & Nislow, 2005). Thus, for some spawner behaviors, parameters determining population productivity and carrying might be influenced if the SR assumption of homogenous distribution of spawning individuals is violated.

In particular, the transfer or extrapolation of SR processes (i.e. maximum reproductive rates and carrying capacities) from one spatial scale to another can be problematic (Mayor et al., 2009), since patterns observed on one scale may not necessarily represent patterns at other scales (Levin, 1992). Data used for population-scale SR estimates commonly represent a sum of many local nonlinear processes affected by multiple local productivity parameters. Available SR data typically consists of numbers or biomass of the spawning stock and resulting recruits; thus, different survival rates that may affect intermediate life stages (e.g. alevin and fry) are often unknown and subsumed into one estimated parameter. For example, density dependent regulatory processes act most strongly in the initial life-stages on restricted temporal and spatial scales (Fernández-Bellon et al., 2016; Finstad et al., 2009; Ray & Hastings, 1996; Rogers et al., 2017). A pre-recruit multi-stage model approach has been suggested to deal with the differences in density-dependent and -independent survival in different life-stages, which might improve the predicted number of recruits in a system (Brooks et al., 2019). Moreover, incorporating local rather than global density dependence in stock assessments is anticipated to provide a better understanding of the effects of fishing on spatially structured populations (Kapur et al., 2021). However, even if local SR parameters are known for all habitats in a system, SR estimates for the whole population might still be biased, if the distribution of spawners among those habitats is ignored. Density-dependent processes might thus act under lower or higher than expected densities if spawner distributions deviate from the common SR assumption that productivity is not affected by the spatial distribution of spawners.

In this study, we study how population productivity might be affected by the underlying habitat selection patterns of spawning individuals. Moreover, we evaluate potential bias in estimates of recruitment and maximum survival rate over a range of population abundance, with and without realistic levels of measurement error, and what implication this might have in stock assessment context. Specifically, we have investigated if different spawner behaviors may introduce bias in estimates of recruitment as well as in SR parameter estimates, and how such bias might vary over population densities. This has been evaluated earlier, using the number of local spawning habitats as a proxy for the total carrying (Maunder & Deriso, 2013), but here we instead use local spawning area and local pre recruited survival rates as potential production capacity limitations. Using the widespread Ricker and Beverton-Holt SR relationships applied to multiple discrete habitats, we compare simulated/expected and estimated total recruitment under four hypothetical spawner behaviors (*habitat quality*, *ideal free*, *random* and *stepwise*; definitions below). Following the spatial dispersal classifications from Thorson et al. (2016) and Bartolino et al. (2011), the habitat quality distribution would fit a constant density model, whereas the stepwise and ideal free distributions fit an proportional distribution model. The random distribution model does not fit any of the suggested distribution models, since distribution is not dependent on spawner abundance.

2 | MATERIALS AND METHODS

Simulated data was produced to quantify potential bias in estimates of total recruitment (R'), total carrying capacity (K') and maximum survival rate (S') relative to underlying predetermined values, using two traditional SR-functions (Beverton & Holt, 1957; Ricker, 1954). The SR-functions used in this study do not account for density dependent mortality caused by predator behavior.

To disentangle the effects of the spawner behavior from other potential sources of bias (i.e. measurement error), and to achieve good contrast in the population abundance data, we first simulated data without additional measurement errors for a wide range of spawner abundances with a maximum close to carrying capacity. Second, to explore how potential effects of spawner behavior would manifest under a more realistic management scenario, we added measurement error and to a subset of the simulated recruitment data (only at lower spawner abundance levels). The simulations consisted of the following six steps:

1. Creation of different environments that define properties of local spawning sites, with randomly assigned habitat characteristics in terms of pre-recruitment survival rates and carrying capacities.
2. Allocation of females to different spawning sites based on the four spawner behaviors evaluated and site-specific environments.
3. Simulation of a recruits at each local site and under each spawner behavior, given the number of females present, using either the Beverton-Holt or the Ricker functions.
4. Calculation of a predefined total carrying capacity and survival rate, using the local spawning site characteristics defined at step 1.
5. Estimation of the parameters for the two stock-recruit functions and the total recruitment, using the total number of females over the entire population abundance range and the total recruitment.
6. Quantify the relative estimation bias (REB) as the difference between the estimated and the predefined: recruitment, survival rate and carrying capacity.

This procedure was then repeated for the measurement error and low abundance scenario using the same set of local parameter values. Each step is described in detail below.

2.1 | Environments

In the equations and text that follow, subscript i denotes spawning site, j denotes the environment, and k denotes the spawner abundance level. In total, the simulations comprised 1000 different environments. Each spawning environment was assigned a unique set of local survival parameter, $S1_{i,j}$ and carrying capacity $K_{i,j}$, but was assumed to have the same female fecundity (Fec), array of total female numbers (N_{tot}, range 100–50,000), and density-independent egg-juvenile survival, $S0$ (see Table 1 for definitions of parameters and variables). The stock-recruit functions (Beverton-Holt and Ricker) introduce density-dependent mortality, which increases with an increasing number of spawners, and therefore the total survival rate will only reach $S0$ in situations with very few eggs.

In each environment, there were five local spawning sites that the spawners could choose from (according to each evaluated spawning behavior). Each spawning site was associated with its own density-independent survival $S1_{i,j}$ and carrying capacity $K_{i,j}$. $S1_{i,j}$ covers the spawning site-specific survival rate from juvenile to recruited individual leaving the spawning and nursery environment (e.g. river, seagrass meadow or bay). The sites were numbered from 1 to 5 with no. 1 having the highest density-independent survival rate, $S1_{1,j}$, followed by lower rates such that $S1_{5,j} < S1_{4,j} < S1_{3,j} < S1_{2,j} < S1_{1,j}$. $K_{i,j}$ parameters were randomly drawn from a Dirichlet-multinomial distribution with a fixed total sum of K $i = 1$ to $5,j$ (150,000) for each environment and with the same underlying probability parameter ($\alpha = 1$) for all spawning sites.

The environments were assumed constant over time, whereas the total number of females varied between years. It did not matter to the simulations in what order the total female numbers appeared;

TABLE 1 Definitions of terms, parameters and variables used in the simulations. The same parameter settings were used for all four spawner behaviors

Parameter	Values	Definition	Explanation
Environment	1–1000	Unique combinations of maximum survival rates and carrying capacity	The environment within which the population spawns. Each environment has five spawning sites
Spawning site	1–5	Five spawning sites per environment	Local spawning site. Each spawner selects one out of five available sites
$R_{i,j,k}$	Varying, calculated	Local recruitment	Based on the underlying spawner behavior, the SR function and $N_{tot,k}$
$R_{tot,j,k}$	Varying, alculated	Total recruitment	The sum of recruitment from all spawning sites for the total spawner abundance
$N_{i,j,k}$	Varying, predefined	Local female abundance	Local female abundance at each spawning site based on the spawner behavior for each $N_{tot,k}$
$N_{tot,k}$	Varying, predefined	Two arrays covering different total numbers of spawners per environment	Without measurement error: sequence of 49 abundances from 100–50,000. With measurement error: sequence of 24 abundances >1 but $<K_{tot,j}/2$
$S0$	0.20	Same at all sites and for all environments	Density-independent egg-juvenile survival rate
$S1_{i,j}$	0.05–0.30	Randomly drawn from a uniform distribution between 0.05–0.3 for each spawning site	Density-independent survival rate covering the juvenile (including potential migration) phase
$K_{i,j}$	$0 < K_{i,j} < K_{tot,j}$	Randomly drawn from a Dirichlet multinomial distribution with a fixed total sum of local $K_{i,j}$ (150,000 recruits) and with equal underlying probability parameter ($\alpha = 1$) for all spawning sites	Local carrying capacity
$K_{tot,j}$	150,000	Different depending on the SR function but the same for all environments	Total maximum carrying capacity in the environment, i.e. the sum of carrying capacities from the five local spawning sites
Fec	5000	Constant for all female spawners	Fecundity (number of eggs per female)
$logsd_{m,j}$	0, 0.2, 0.4, 0.6	SD (of log(x)) for lognormal measurement errors	SD of lognormal measurement errors added to $R_{tot,j,k}$ in the simulations with low spawner abundance levels
χ_j	Varying, predefined	$\chi_j = \sum_{i=1}^{n} S1_{i,j} K_{i,j}$	Predefined maximum number of recruits for the environment j
$\Theta_{j,k}$	Varying, predefined	$\theta_{j,k} = \frac{\sum_{i=1}^{n} R_{i,j,k}}{\sum_{i=1}^{n} \frac{R_{i,j,k}}{S1_{i,j}}} S0$	Predefined total survival rate for the environment j and spawner abundance k
$R'_{j,k}$	Varying, estimated	Estimated total recruitment	Total recruitment estimated based on the number of recruits for spawner abundance k and environment j. Calculated from the SR functions using the estimates of S_j' and K_j'
K_j'	Varying, estimated	Estimated total carrying capacity	Estimated total (summed over all sites) carrying capacity in the environment j. Estimated from the entire range of simulated SR data
S_j'	Varying, estimated	Estimated total survival rate	Estimated total survival rate in environment j. Estimated from the entire range of simulated SR data
$\omega_{tot,j,k,m}$	Varying, calculated	Total recruitment with measurement error	Total recruitment with additional measurement error with SD m

the actual years were not relevant to the results and were therefor omitted from the analyses. Hence, the dynamics of the populations are not modeled explicitly.

For each environment, two one-dimensional arrays of female numbers were used. The first array contained 49 different total female numbers, with the highest numbers in a given environment chosen to reach close to $K_{tot,j}$ in the Beverton-Holt stock-recruit function, and to exceed the peak in the Ricker function. The reason for this choice was to allow as good a fit as possible of the global SR function and to isolate the effects of spawner behavior, potentially causing bias in the recruitment estimates as well as in the parameter estimates. The second array consisted of 24 different equally spaced total female numbers, with the highest female numbers resulting in a total recruitment corresponding to just half of the total carrying capacity ($K_{tot,j}/2$). This range of data availability was introduced in order to mimic real-life management situations where harvested stocks often exhibit abundance levels far below carrying capacity.

Total recruitment ($R_{tot,j,k}$) was calculated by summing local recruitment from the five spawning sites for each female abundance level after accounting for mortality loss due to $S1_{i,j}$ and $S0$. Local recruitment (for each spawner behavior) was calculated using the Beverton-Holt and the Ricker stock-recruit functions. The Beverton-Holt and Ricker functions were chosen since they are both widely used in stock assessments (Lowerre-Barbieri et al., 2017; Myers, 2001; Walters & Martell, 2004), and moreover, since they cover two different compensatory shapes: asymptotic compensation (Beverton-Holt) and dome-shaped overcompensation (Ricker). The asymptotic compensatory process in the Beverton-Holt function can arise from increasing intraspecific competition, whereas the over-compensatory Ricker shape can be induced by cannibalism. There are other extensions of the Ricker and Beverton-Holt SR functions that account for additional ecological theories (e.g. Maunder & Deriso, 2013; Taylor et al., 2013). The SR functions used in this study do not account for density dependent mortality caused by predator behavior.

We chose to parameterize both the Beverton-Holt and Ricker functions using the peak level of recruitment ($K_{i,j}$) (Pulkkinen & Mäntyniemi, 2013; Quinn & Deriso, 1999):

$$R_{i,j,k} = \frac{S1_{i,j}\ S0\ N_{i,j,k}\ Fec}{1 + S0\ N_{i,j}, k\ Fec\,/\,K_{i,j}}, \qquad (\text{Beverton} - \text{Holt})$$

$$R_{i,j,k} = S1_{i,j}\ S0\ N_{i,j,k}\ Fec\ e^{-\frac{S0\ N_{i,j,k}\ Fec}{e\ K_{i,j}}}, \qquad (\text{Ricker})$$

where $R_{i,j,k}$ is the local recruitment and $N_{i,j,k}$ is local female abundance. Carrying capacity, $K_{i,j}$, can be thought of as the theoretical maximum recruitment the stock could obtain with maximum survival. Note that this differs from $R0$, another common parameterization defined as the long-term average recruitment at demographic equilibrium with no fishing, as R_0 also includes information about the unfished eggs or spawning biomass per recruit. The ratio of R_0 to $K_{i,j}$ depends on the stock-recruit steepness: thus use of $K_{i,j}$ is analogous to the use of R_0 in situations where steepness approaches one. The relationship between R_0 and $K_{i,j}$ is described as:

$$R_{0,i,j} = \frac{K_{i,j}\left(EPR0 - \frac{1}{S1_{i,j}S0}\right)}{EPR0},$$

where $EPR0$ is unfished eggs per recruit, which in our study would be Fec, since we assumed constant mean fecundity in all simulations.

2.1.1 | Spawner behaviors

The four spawner behaviors evaluated are defined as follows:

1. Preference for habitat quality, HabQ

The spawners' probability to select a local spawning site is directly proportional to the local habitat quality in terms of its carrying capacity compared with the other sites. In this scenario, the females will spread among the five local spawning sites such that the relative frequency distribution of spawners at the five sites becomes equal to the relative frequency distribution of the five carrying capacities. Note that this spawner behavior is not similar to what would be expected in a dynamic situation, at equilibrium, when the offspring returns to the site where they were born, as the HabQ behavior does not account for offspring migration mortality. The number of spawners in each local spawning site was calculated as:

$$N_{1,j,k} = \left(\frac{K_{1,j}}{\sum_{i=1}^{n} K_{i,j}}\right)N_{tot,k}, N_{2,j,k} = \left(\frac{K_{2,j}}{\sum_{i=1}^{n} K_{i,j}}\right)N_{tot,k}, \ \dots\ N_{n,j,k} = \left(\frac{K_{n,j}}{\sum_{i=1}^{n} K_{i,j}}\right)N_{tot,k}$$

where $N_{tot,k}$ is the total female abundance for the spawner abundance level k.

2. Ideal free distribution, IFD

Following an ideal free distribution, each spawner selects the spawning site that will maximize the overall per capita (Fretwell & Lucas, 1970). The first spawners will select the habitat with the highest product of $S1_{i,j}{*}K_{i,j}$, but as the number of spawners increase and density dependence starts to reduce the recruitment success the habitat choice will depend on the number of spawners already present at the different spawning sites. The solution in this situation can only be found by comparing the expected per capita recruitment success, $R_{i,j,k}\,/\,N_{i,j,k}$, at each spawning site. When there are many spawners the final distribution will be the one when the per capita recruitment is approximately the same at all spawning sites. At equilibrium the IFD will be identical to a strict homing spawner behavior (i.e. that spawners return to the same local site as where they were born), in terms of the number of spawners at each habitat, and in terms of individual fitness. The IFD process was solved iteratively so that each additional spawner "evaluated" the recruits/egg ratio based on the existing spawner densities at each spawning site.

3. Random habitat selection, Random

We used the Dirichlet-multinomial distribution to distribute the spawners randomly among the five spawning sites:

$$N_{1,j,k}, N_{2,j,k} \dots N_{n,j,k} \sim Dirichlet-Multinomial\left(1, 1, \dots 1, N_{tot,k}\right).$$

With this function, the selection of spawning site is essentially random among the first spawners that arrive. With no influence from local habitat quality, whereas at an increased abundance spawners select sites in proportion to, approximately, twice the number of spawners already available at the sites. Hence, the distribution of spawners among sites starts to deviate from equal probabilities as the number of spawners increases. This means that the random distribution will seldom result in an equal distribution of spawners among the five sites. Moreover, the same distribution pattern is unlikely to be repeated in subsequent spawnings since the site that attracts many spawners is a random process.

4. Stepwise habitat selection, Stepwise

The stepwise habitat selection pattern was based on the theory of social attraction (Bietz, 1981), and the empirical study by Finstad et al. (2013), who showed that Atlantic salmon (Salmo salar) preferred areas used by other spawners, and that utilization of additional spawning sites was positively correlated with spawner densities. Under a stepwise habitat selection pattern, the closest (e.g. farthest downstream) spawning site (no. 1) will be used first until a fixed abundance threshold is reached, after which the next closest spawning site (no. 2) will be utilized, and so on until all habitats are filled. Then additional spawners are distributed equally among all spawning areas. The abundance threshold was set to 95% of $K_{i,j}$, and equal for all spawning sites.

The influence of the different spawner behaviors on the distribution of females among the five sites and on the total recruitment is illustrated in Figures 1, 2.

2.2 | Parameter values used in the simulations

Values and limits for the predefined parameters were chosen arbitrarily, but are based on production parameters seen as realistic for a salmonid fish (according to expert opinion), Definitions and parameter values are listed in Table 1.

2.2.1 | Predefined parameter values

The predefined simulated parameter value for the maximum total recruitment for environment j, χ_j, was defined as:

$$\chi_j = \sum_{i=1}^{n} S1_{i,j} K_{i,j}.$$

Predefined total survival rate in the system ($\Theta_{j,k}$) was based on the five local survival rates ($S1_{i,j}$) and the initial survival rate ($S0$) for each spawner abundance level, and was calculated as the product of total $S1_j$ and S0 as:

$$\theta_{j,k} = \frac{\sum_{i=1}^{n} R_{i,j,k}}{\sum_{i=1}^{n} \frac{R_{i,j,k}}{S1_{i,j}}} S0,$$

where total $S1_{i,j}$ is defined as the ratio of the total number of recruits based on the total $S1_{i,j}$ and $S0$ ($\sum_{i=1}^{n} R_{i,j,k}$) and the total number of recruits with only $S0$ ($\sum_{i=1}^{n} R_{i,j,k} / S1_{i,j}$).

2.2.2 | Parameter estimation

For each of the four modeled spawner behaviors, the parameters K_j' (maximum recruitment in the environment) and S_j' (maximum survival rate in the environment) were estimated using the complete spawner abundance sequence ($N_{tot,j}$, $n = 49$ or 24).

We estimated combined S_j' survival rate and carrying capacity, K_j', for the Beverton-Holt model as:

$$R_{tot,j,k} = \frac{S_j{}'N_{tot,j,k}Fec}{\left(1 + S_j{}'N_{tot,j,k}Fec / K_j{}'\right)},$$

and for the Ricker model as:

$$R_{tot,j} = S_j{}'N_{tot,j,k}Fec\, e^{-\frac{S_j{}'N_{tot,j,k}Fec}{eK_j{}'}}.$$

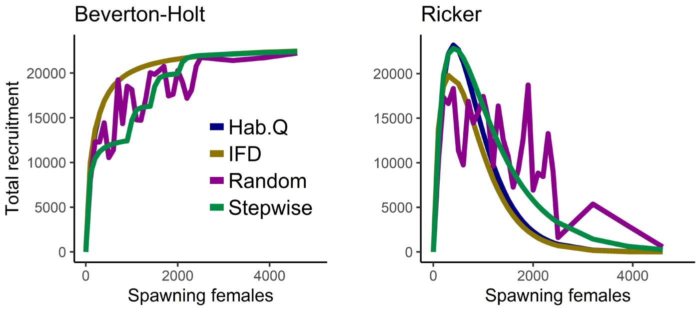


FIGURE 1 Conceptual figure showing differences in stock-recruitment relationships for four different spawner distribution behaviors, assuming local Beverton-Holt (left) and Ricker SR-relationships (right). Spawners (females) and recruits have been summed across five local spawning sites. See text for details.

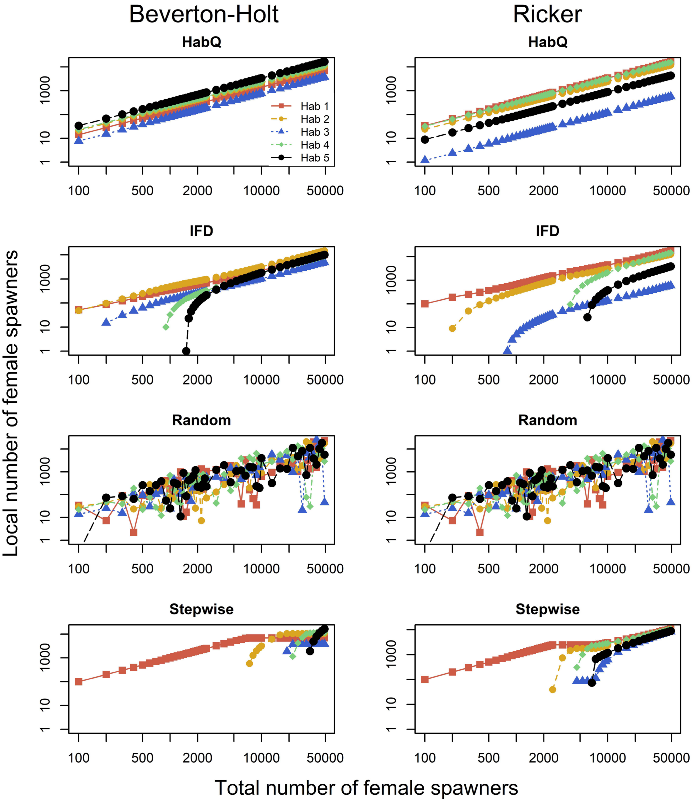


FIGURE 2 Total female abundance compared with the number of females at five local spawning sites with a common environment (environment 1). Panels represents combinations of the four spawner behaviors (rows) and two SR relationship (columns). Note that the two axes are shown on logarithmic scales.

Note that only one survival parameter was estimated, to resemble realistic stock assessment use of the SR functions where most often one density-independent survival parameter (alpha) is estimated. S_j' here represented the combined survival rate from egg to recruit (i.e. $S0$ and $S1_{i,j}$) as with $\Theta_{j,k}$. Note also that the predefined survival rates ($\Theta_{j,k}$) are defined for each spawner abundance level (that can imply a different distribution of spawners across sites), while the estimated survival rate does not depend on the spawner abundance. The parameters were estimated via non-linear least squares regression using the "nls_multstart" function from the nls.multstart package in R (Padfield & Matheson, 2018). This function requires upper and lower starting values for the parameters estimated; upper and lower values were set to 0.001 and 0.1 for the S_j' parameter and to 10,000 and 40,000 for the K_j' parameter. These limits for the K_j' parameter were chosen since the maximum total recruitment in an environment would be a function of $S1_{i,j}$ (Table 1). Thus, the maximum total recruitment in the environment would not be the sum of the total $K_{i,j}$ (150,000).

2.2.3 | Relative estimation bias

The relative estimation bias (REB) was calculated as the difference between the estimated parameter values for K_j' and S_j', calculated from the SR data for the entire spawner abundance range, and their corresponding predefined values (χ_j and $\Theta_{j,k}$), divided by the predefined parameter values, where positive and negative values indicate over- and under-estimation, respectively. REB for R_j' was calculated as the difference in percent between the estimated recruitment (based on the SR curves obtained when applying the estimated S_j' and K_j' in the SR functions), and the observed recruitment from the simulations for the total range of spawner abundance. The SR data, analysis, parameter estimates and figures were executed and produced in R version 4.2.1 (R Core Team, 2022).

2.3 | Measurement error and data availability for management situations

Based on the same 1000 environments 24 equally spaced spawner abundance levels were produced from a spawner abundance between 1 and $K_{tot,j}/2$ where additional lognormal measurement error was added to the total recruitment for each spawner behavior, spawner abundance level and the two SR functions. In this simulation, the predefined parameter values for each environment were the same as above, and the REB calculations were made using the same predefined values of recruitment $R_{tot,j,k}$, $\Theta_{j,k}$ and χ_j. Since a Ricker SR curve has two levels of spawner abundance representing $K_{tot,j}/2$, the upper limit was set to $K_{tot,j}$ and below in order to exclude levels of spawner abundances above the peak. To mimic realistic levels of measurement error, lognormal random variates with an SD of 0, 0.2, 0.4 or 0.6 were added to each observed total recruitment for each environment:

$$\omega_{tot,j,k,m} = Lognormal\left(mean = \log\left(R_{tot,j,k}\right), \sigma = logsd_m\right),$$

where $logsd_m$ is the standard deviation of the lognormal distribution (SD of log(x)), and *m* indexes different magnitudes of measurement error (SD = 0, 0.2, 0.4 or 0.6), where SD = 0 depicted estimates without measurement error. Measurement errors typically depend on the type of observation/data and the process by which they are sampled or measured, and have been suggested to be around 60% among several orders of marine fishes (Thorson et al., 2014). However, a range between 0% and 20% measurement error is often sufficient to explore the consequences of both small and large measurement error in fisheries ecology (Memarzadeh et al., 2019), which is why we also included intermediate levels of measurement errors. Walters and Ludwig (1981) showed that lognormal measurement errors introduce bias in the stock-recruit estimates as well as in the parameter estimates, and that this bias could be removed by multiplying with a correction term, $\exp(-1/2\ \sigma^2)$. In this study, we applied this correction factor in order to analyze the bias introduced by the behaviors rather than that introduced by the lognormal measurement error.

3 | RESULTS

The total recruitment and the SR parameters were affected by the spawning behavior, where the magnitude and variation in the REB dependent on the specific spawner behavior.

3.1 | Relative estimation bias without measurement error and full range of spawner abundance

In general, the estimates of recruitment (R_j') and the two parameters S_j' and K_j' were affected by the underlying spawner behavior, but the magnitude of observed bias (REB) was largely dependent on the distribution behavior (Figures 3, 4).

3.2 | HabQ

Across environments, the HabQ spawner selection behavior did not introduce any bias in the prediction of total recruitment (R_j') or in the estimates of S_j' and K_j' (Figures 3, 4). This was consistent for both the Beverton-Holt and the Ricker function (Figures 3, 4).

3.3 | Ideal free distribution

With a Beverton-Holt SR relationship, IFD spawner behavior caused larger bias in the estimated R_j', S_j' and K_j' compared with the HabQ spawner behavior (Figure 3). However, the REB in the K_j' parameter estimate was close to zero and constant over the full range of spawner abundance (Figure 3). Meanwhile, estimates of R_j' and S_j' introduced larger REB that was not constant over the spawner abundance range, indicating that with a Beverton-Holt SR relationship the REB for these two estimates were dependent on the spawner abundance, where most REB was introduced at low spawner abundance levels (Figure 3).

Also with a Ricker SR relationship, the HabQ spawner behavior produced negligible REB, whereas with an IFD spawner behavior REB was almost twice as large on average compared with the Beverton-Holt SR relationship (Figure 4). The REB in the R_j' and S_j' estimates varied over the spawner abundance range, whereas the REB introduced in K_j' estimates was constant (Figure 4). As for the Beverton-Holt SR, a Ricker SR relationship introduced most REB for the R_j' and S_j' at low spawner levels, whereas the median REB at high spawner abundance was close to zero (Figure 4).

3.4 | Random

The random spawner behavior introduced a large REB with significant variation compared with the other three spawner behaviors (Figures 3, 4). This was consistent for both the Beverton-Holt and the Ricker SR functions. The estimates of R_j' were in general dependent on the spawner abundance, whereas the REB in the K_j' and S_j' was constant and independent of spawner abundance (Figures 3, 4). For the estimates of the parameters K_j' and S_j' virtually all of the REB was below zero, which means that in almost all environments these two parameters would be underestimated for a random type of spawner behavior (Figures 3, 4).

3.5 | Stepwise

For both SR relationships, the stepwise spawner behavior introduced REB in the estimates of R_j', following the same pattern as for the other three spawner behaviors, with larger REB at low spawner abundance and REB close to zero at high spawner abundance (Figures 3, 4). However, the REB in the estimates of R_j' with a Ricker SR relationship dropped off at high spawner abundance (Figure 4). This means that for population abundances above the peak of the Ricker curve we would underestimate total recruitment. The REB in the estimates of S_j' were virtually independent of spawner abundance (constant) for the Beverton-Holt SR relationship (Figure 3), but dependent on spawner abundance in the Ricker SR relationship (Figure 4). The REB for the K_j' estimates were in general overestimated, for both a Beverton-Holt and a Ricker SR relationship (Figures 3, 4), but without any trends across the full range of spawner abundance.

3.6 | Relative estimation bias at low population abundance, with and without measurement error

For the analysis of REB at lower population abundances and different levels of measurement error, the results are presented both graphically (Figures 5–10) and as numbers (Table 2). The figures presented in the main manuscript compare REB introduced by zero measurement errors (i.e. only spawning behavior), and REB introduced by measurement errors with SD = 0.2, 0.4 and 0.6 (i.e. spawning behavior and added measurement error) for the Beverton-Holt (Figures 5–7) and Ricker SR functions (Figures 8–10).

Even if additional measurement error affected the magnitude of the REB, the different spawner behaviors influenced the REB differently, and for some of the spawner behaviors, the spawning behavior explained most of the REB (Figures 5–10, Table 2). What was most

TABLE 2 Mean and SD of the median REB for the estimated R', S' and K' based on additional measurement errors at different levels (SD) under Beverton-Holt and Ricker SR relationships

Spawner behavior	Measurement error (SD)	R'		S'		K'	
		Mean	SD	Mean	SD	Mean	SD
Beverton-Holt							
HabQ	0	0.00	0.00	0.00	0.00	0.00	0.00
	0.2	0.021	0.070	0.010	0.19	0.040	1.80
	0.4	0.087	0.17	0.10	0.51	0.090	434.25
	0.6	0.22	0.32	0.26	6.51	0.22	44747.62
IFD	0	−0.010	0.010	−0.060	0.070	−0.090	0.12
	0.2	0.020	0.070	−0.040	0.20	−0.11	1.12
	0.4	0.090	0.17	0.060	0.49	−0.090	127.36
	0.6	0.19	0.32	0.13	115.95	0.060	5231.92
Random	0	−0.03	0.29	−0.32	Inf	−0.17	0.22
	0.2	0.00	0.32	−0.29	0.44	−0.16	0.53
	0.4	0.07	0.38	−0.25	138.87	−0.090	4.91
	0.6	0.19	0.53	−0.18	2.41×10^{7}	0.00	51.040
Stepwise	0	−0.01	0.26	−0.64	Inf	−0.41	Inf
	0.2	0.01	0.29	−0.64	0.85	−0.41	8865.13
	0.4	0.07	0.35	−0.63	467.88	−0.36	8962.090
	0.6	0.20	0.51	−0.60	8.53×10^{6}	−0.27	56899.65
Ricker							
HabQ	0	0.00	4.12×10^{-6}	2.11×10^{-7}	3.56×10^{-6}	-8.02×10^{-7}	1.20×10^{-5}
	0.2	0.030	0.070	0.040	0.14	−0.010	45.83
	0.4	0.11	0.18	0.12	0.30	0.12	631.36
	0.6	0.26	0.35	0.34	0.70	0.040	597.00
IFD	0	−0.010	0.010	−0.050	0.070	−0.28	0.31
	0.2	0.010	0.080	−0.030	0.15	−0.31	5.35
	0.4	0.080	0.18	0.050	0.29	−0.27	85.67
	0.6	0.21	0.33	0.19	0.57	−0.22	139.93
Random	0	−0.030	0.51	−0.20	0.32	−0.42	Inf
	0.2	0.010	0.55	−0.19	0.34	−0.38	2.37
	0.4	0.080	0.65	−0.13	0.41	−0.34	14.030
	0.6	0.21	0.89	−0.030	0.71	−0.25	57.040
Stepwise	0	−0.030	0.050	−0.23	0.27	−0.35	Inf
	0.2	0.00	0.09	−0.20	0.27	−0.32	18.38
	0.4	0.070	0.18	−0.15	0.31	−0.27	90.43
	0.6	0.22	0.37	0.010	0.51	−0.20	360.020

Note: Estimates only for lower ranges of spawner abundances ($\leq K_{tot,j}/2$). Inf (infinity) values were obtained when the exponential part of the SD calculation gave inf. Large numbers.

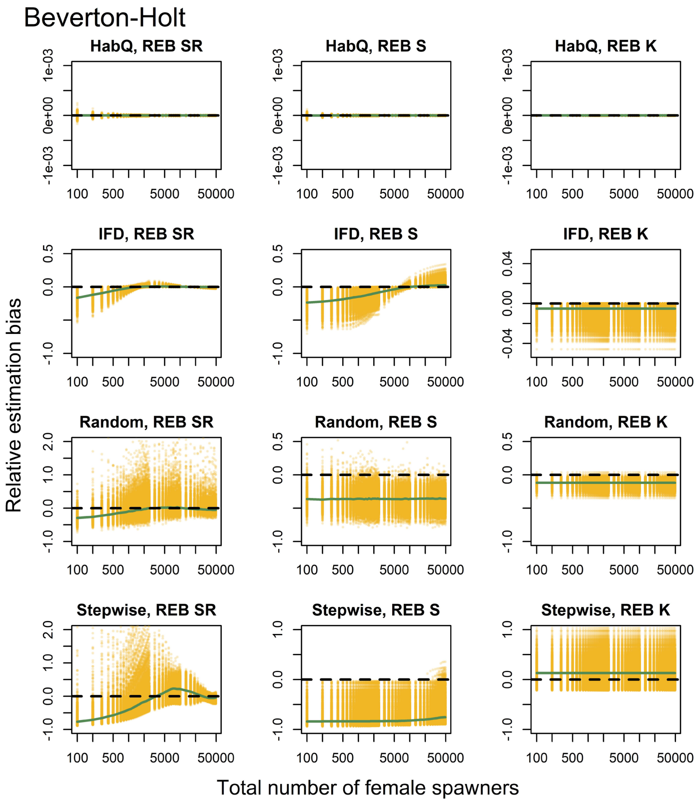


FIGURE 3 The REB for the total recruitment R', survival rate S' carrying capacity K', for a Beverton-Holt SR relationship. Each row represents one of the four different spawner behaviors evaluate (HabQ, IFD, random, stepwise). Each yellow dot represents REB calculated for a specific combination of an environment and a total spawner abundances. Green solid lines show the median REB calculated for each spawner abundance level from all of the 1000 environments. Solid black lines illustrate zero REB. Positive and negative values of REB indicate over-/underestimation of the known parameter values and total recruitment. Note that the total number of female spawners (x-axis) is shown using a logarithmic scale.

interesting was that the average REB for the R_j' was more or less equal for the four different spawner behaviors and SR functions, whereas the average REB in K_j' and S_j' was higher for stepwise and random spawner behaviors (Table 2). Moreover, the average REB in K_j' and S_j' estimates was increased with increasing levels of measurement error for HabQ and IFD spawner behaviors, whereas the average REB decreased with increasing levels of measurement error for the stepwise and random spawner behaviors (Table 2).

3.7 | HabQ

For a HabQ spawner behavior, measurement error with SD = 0.2, 0.4 and 0.6 explained the majority of the REB for the estimated R_j', S_j' and K_j' (Table 2). This was consistent for both the Beverton-Holt and the Ricker SR relationship (Figures 5–10). In Figures 5–10, this is visualized by the majority of the visible points being black. This means that for stocks with a HabQ type of spawner behavior, data containing low spawner abundance, and measurement error (SD ≥0.2); the measurement errors will generate larger REB than the underlying spawner behavior.

3.8 | Ideal free distribution

For an IFD spawner behavior, all three levels of measurement error resulted in a large variation in the REB of R_j', S_j' and K_j' (Figures 5–10, Table 2). Both the median REB and the variation in REB were larger than what was produced by the underlying spawner behavior (zero measurement error) (Figures 5–10, Table 2). These results were consistent for both SR relationships. In estimates of R_j' and S_j' the REB was influenced by the spawner abundance (Figures 5–10), where larger REB was introduced at low spawner abundance.

3.9 | Random

For a random spawning behavior and a moderate measurement error (SD = 0.2), most of the REB in R_j', S_j' and K_j' were explained by the spawner behavior. This was consistent for both SR relationships (Figures 5, 8). However, increased measurement error (SD > 0.2) generated larger and more variable median REB (Figures 6, 7, 9, 10, Table 2). For all levels of measurement error, the REB was constant over the spawner abundance range, which means that the REB was not dependent on the abundance

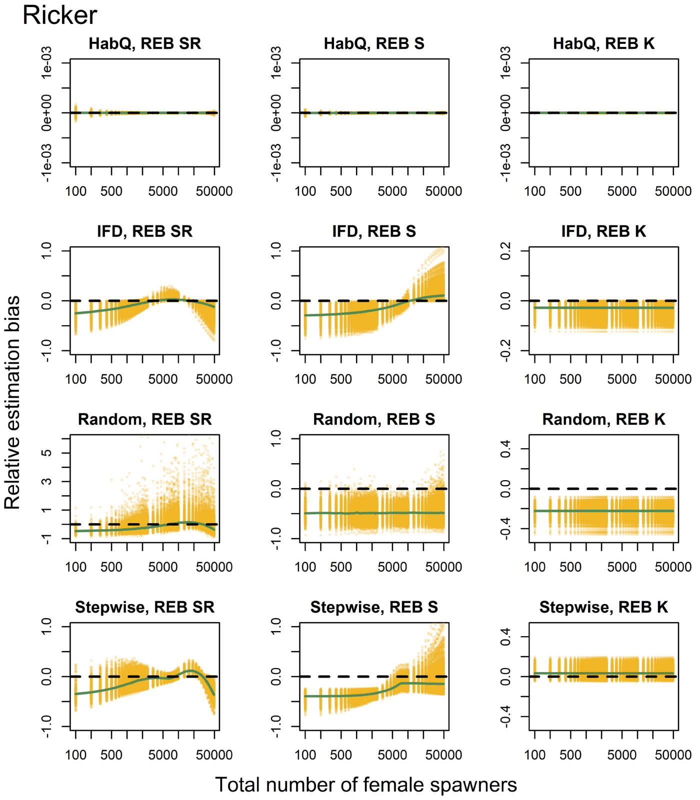


FIGURE 4 The REB for the total recruitment R', survival rate S' carrying capacity K', for a Ricker SR relationship. Each row represents one of the four different spawner behaviors evaluate (HabQ, IFD, random, stepwise). Each yellow dot represents REB calculated for a specific combination of an environment and a total spawner abundances. Green solid lines show the median REB calculated for each spawner abundance level from all of the 1000 environments. Solid black lines illustrate zero REB. Positive and negative values of REB indicate over-/underestimation of the known parameter values and total recruitment. Note that the total number of female spawners (x-axis) is shown using a logarithmic scale.

level. Compared with the IFD and HabQ the random spawner behavior introduced a larger median REB in estimates of S_j' (Figures 5–10).

3.10 | Stepwise

For a stepwise spawner behavior and a majority of the REB in estimated R_j' was explained by the spawner behavior compared with measurement error (SD = 0.2, 0.4 and 0.6, Figures 5–10, Table 2), except for a Ricker SR relationship with SD = 0.6 (Figure 10, Table 2). The estimates of S_j' was also largely influenced by the spawner behavior at low measurement error (SD = 0.2), whereas larger measurement error (SD = 0.4 and 0.6) generated high variation in REB (Figures 5–10, Table 2). Even if the median of the REB in the estimated S_j' was almost equal between the different measurement error levels (SD = 0, 0.2, 0.4 and 0.6), REB without measurement error (SD = 0) introduced REB that was almost exclusively negative, whereas the other three levels of measurement error introduced both negative and positive REB (Figures 5–8, Table 2). Estimates of K_j' introduced large variations in REB, independently of the SR relationship and spawner abundance level (Figures 5–10, Table 2).

4 | DISCUSSION

Two of the spawner behaviors evaluated (HabQ and IFD) introduced no or negligible bias in the estimates of total recruitment, survival rate and maximum potential recruitment, whereas the other two spawner behaviors (random and stepwise) generated considerable REB. These results were consistent for both the Beverton-Holt and Ricker SR relationships. These general results were also consistent with and without additional bias (i.e. measurement error). Our results, therefore, suggest that for some underlying spawner behaviors the SR relationship might not be well approximated even when local recruitment is based on one of these two functions. Depending on the habitat selection pattern, this miss-specification might ultimately yield biased parameter estimates for two extensively used SR functions (i.e. Beverton-Holt and Ricker).

For the two common SR functions studied herein, spawning individuals in the population are typically assumed to distribute homogeneously across all potential spawning sites in a system, with all offspring suffering the same average mortality independent of where they were born. These assumptions are probably not realistic for most fish species, and there are studies suggesting alternative spawner behaviors for at least some species (Bouchard et al., 2018;

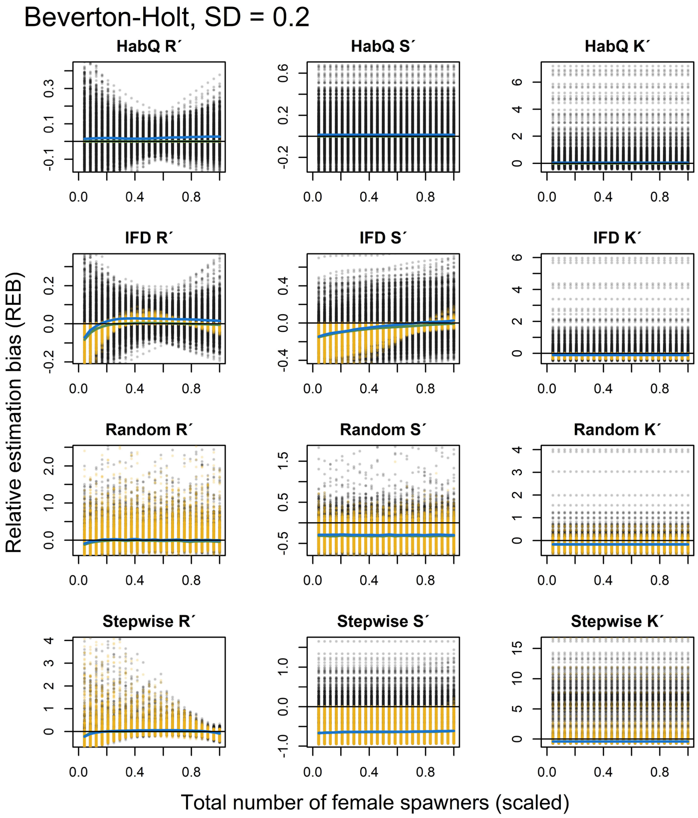


FIGURE 5 REB for R', S' and K', based on low spawner abundance ($K_{tot,j}/2$) without (yellow dots) and with added measurement error (SD = 0.2, black dots), for a Beverton-Holt SR relationship. Green and blue solid lines show the median REB without and with measurement error, respectively. Black solid line shows zero REB. Note the different scales on the Y-axis. For clearer visualization, female abundance (x-axis) is displayed as a proportion of the evaluated maximum abundance.

Falcy, 2015; Finstad et al., 2013; Haugen et al., 2006; Huntsman et al., 2017; MacCall et al., 2019). The four distribution patterns evaluated in this study are perhaps rough simplifications of the real world, but our results clearly demonstrate that depending on the spawner behavior in combination with environmental conditions in terms of density-independent survival rates and carrying capacities, estimates of population productivity can be biased using these two common SR functions´.

When the spawner behavior was proportional to the local carrying capacities (i.e. HabQ distribution), parameters were estimated with high accuracy and precision over the entire spawner abundance range (i.e. low REB). Under a more realistic management scenario using a lower spawner abundance range and additional measurement error the median estimates of $R´$, $S´$ and $K´$ did not change remarkably, only variation in REB, which could be explained by the level of measurement error that was added. This indicates that under a HabQ spawner behavior, the Beverton-Holt and Ricker SR functions are consistent with the assumption that reproducing individuals distribute in a spawning system according to local carrying capacities, where abundance occupation of all spawning sites is expected even at low spawner abundance (see derivation in Appendix S1). This type of spawner behavior has been observed in chinook salmon (*Oncorhynchus tshawytscha*) where habitat quality can override a strict homing spawner behavior (Cram et al., 2013). However, this relationship no longer holds when S0 differs between habitats. Since S0, among other things includes losses due to predation, one might suspect that S0 differs between spawning areas, and our conclusion of negligible bias in the global SR function for the HabQ behavior might therefore be over-optimistic.

The Ideal free distribution has been suggested to hold as the spatial distribution for many marine fish species (Shepherd & Litvak, 2004). Our results show that an IFD spawner behavior generated relatively low REB on average, but with a larger variation compared with the HabQ. It is important to note that each dot in Figures 3–10 represents recruitment from one spawner abundance level in one environment. So a larger variation in REB illustrates that for some environments (habitat parameter settings) we might risk considerable bias if we do not consider the underlying spawner behavior in the SR functions. Moreover, the REB in R' and S' varied over the spawner abundance range, which means that the magnitude of REB was influenced by the spawner abundance level, where

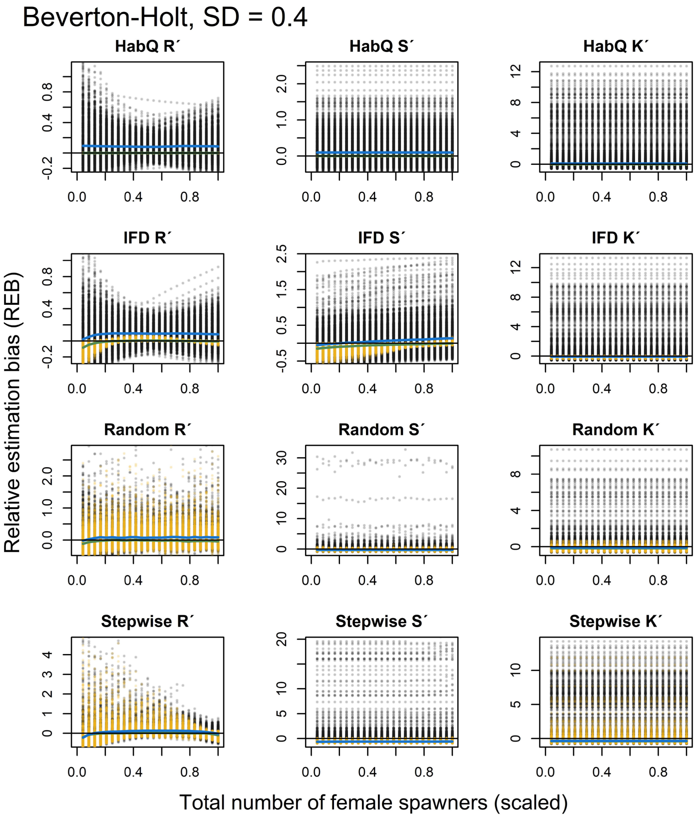


FIGURE 6 REB for R', S' and K', based on low spawner abundance ($K_{tot,j}/2$) without (yellow dots) and with added measurement error (SD = 0.4, black dots), for a Beverton-Holt SR relationship. Green and blue solid lines show the median REB without and with measurement error, respectively. Black solid line shows zero REB. Note the different scales on the Y-axis. For clearer visualization, female abundance (x-axis) is displayed as a proportion of the evaluated maximum abundance.

at low spawner abundance R' and S' were underestimated, but at high spawner abundance levels the REB was almost zero. These results were consistent also when only low spawner abundance range data was used and measurement errors were added. Therefore, for populations at low abundance levels also an IFD might introduce bias in estimates of SR relationships if the spawner behavior is ignored.

The variation and magnitude of REB were more pronounced in the random spawner behavior which is perhaps not surprising since the density in each spawning site was randomly assigned, meaning that some sites were underutilized, whereas others were over-utilized over the full spawner abundance range. This was also reflected in the low spawner abundance data analysis with additional measurement errors added where a large proportion of the variation in REB could be explained by the random behavior, even at the highest levels of measurement errors added (SD = 0.6). Maunder and Deriso (2013) suggested a spatial extent SR function resembling a Beverton-Holt SR relationship that assumed a random distribution of spawners. However, as also Maunder and Deriso (2013) discuss, a random spawner behavior might perhaps not be realistic.

A stepwise spawner distribution is perhaps not a realistic spawner distribution on its own either, but stepwise dispersal in fish has been observed in empirical studies; e.g. reflecting spillover processes (Abesamis & Russ, 2005), spawner dispersal (Finstad et al., 2013) and density-dependent habitat expansion (Bartolino et al., 2011). The stepwise spawner behavior generated a large median REB with considerable variation. This was consistent for all analyses and SR functions. Moreover, the stepwise spawner behavior explained the majority of the variation in REB even when additional measurement error was introduced. These results indicate that in some environments a stepwise spawner behavior may generate estimation bias in vital SR relationship estimates, which should be of concern for stock assessments. A Larger REB was generated in estimates of the maximum survival rate parameter ($S´$), compared with the total carrying capacity (K'). This was consistent using both the full and low spawner abundance range, with and without measurement error added, and for both SR relationships. The high accuracy and precision in the estimates of K' is probably due to that the spawner abundance range was sufficient to inform the SR functions of the peak (Ricker) or asymptote (Beverton-Holt) part of the SR relationship.

Even if K' is essential in SR functions, most exploited fish stocks are probably far from the true carrying capacity of the system, which makes estimates of the S' parameter arguably more important for population dynamics modeling and stock assessment (Myers, 2001). The S' parameter is the initial slope of the SR curve and can be

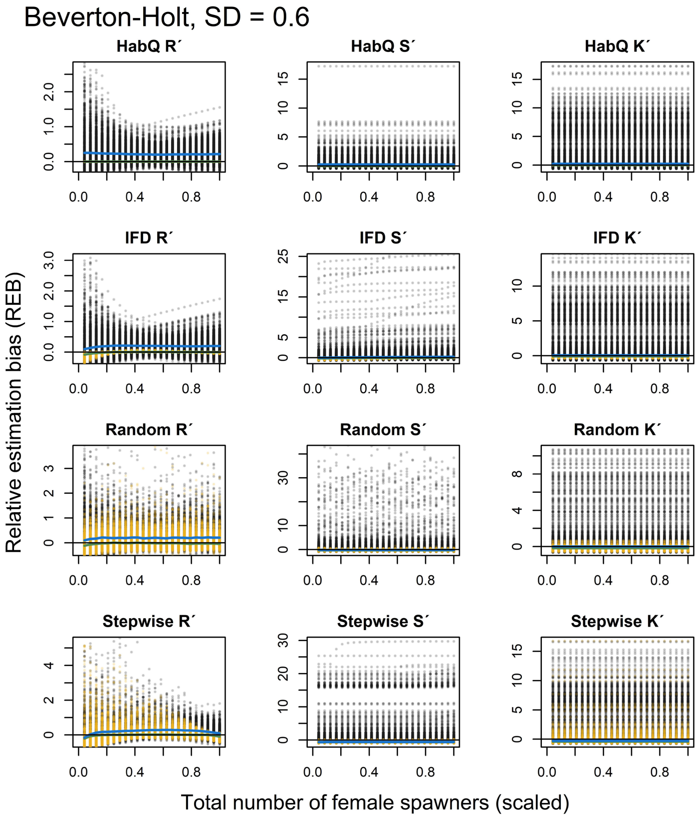


FIGURE 7 REB for R', S' and K', based on low spawner abundance ($K_{tot,j}/2$) without (yellow dots) and with added measurement error (SD = 0.6, black dots), for a Beverton-Holt SR relationship. Green and blue solid lines show the median REB without and with measurement error, respectively. Black solid line shows zero REB. Note the different scales on the Y-axis. For clearer visualization, female abundance (x-axis) is displayed as a proportion of the evaluated maximum abundance.

interpreted as the maximum reproductive rate of a stock, which makes it an important parameter in fisheries assessment and management (Myers, 2001). Our results show that the population-level survival rate is not only affected by spawner behaviors and the SR relationship (Beverton-Holt or Ricker), but also by spawner abundances for a given distribution pattern. As an example, IFD, random and stepwise spawner behaviors generated underestimates of the survival rates at low spawner abundances but negligible REB at high spawner abundance levels. Thus, even if we would have data covering the whole range of population density, we still risk underestimating the survival rate when population abundance declines. Interestingly, the median REB in the survival rate estimates were reduced for a random and stepwise spawner behavior when additional measurement errors were added. The majority of the REB in survival rate was mainly negative and additional measurement error introduced positive REB, which generated a median REB closer to the predefined parameter values. Therefore, measurement errors might in these cases make estimates less biased. Furthermore, for fish species that have both spatially constrained and unconstrained life stages, climate change might induce a further separation in stage-specific habitat usage (Ciannelli et al., 2022). This could lead to a reduction in the habitat range where local spawning sites might be inaccessible or unused in the future.

4.1 | Management perspectives

Even when factors contributing to lifetime reproductive output (e.g. fecundity, maternal age and size structure) are accounted for in SR functions, estimates of recruitment often remain highly variable (Green, 2008). Our results suggest that the distribution of spawners might influence such variability. However, our analysis with additional measurement error, and with SR data covering only low spawner abundance levels, shows that for a HabQ and IFD spawner behaviors, the resulting increase in bias, might mask the effects of the underlying spawner behavior (e.g. generate higher variation in REB than the spawner behavior). Most stock-recruit data sets for managed fish stocks lack contrast in spawner abundances, and rather consist of relatively short time series at low or intermediate spawner abundances (Hilborn & Walters, 2015). Moreover, additional sources of bias, e.g. environmental variation, time-series bias, shifting productivity regimes, and observation and (or) process bias are common in SR data (Haddon, 2001; Maunder & Piner, 2015; Quinn & Deriso, 1999; Vert-pre et al., 2013; Walters, 1985). For stocks lacking contrasting data and with measurement errors (SD > 0.2) the bias caused by the underlying spawner behavior might therefor be of subordinate concern compared with that related to the measurement

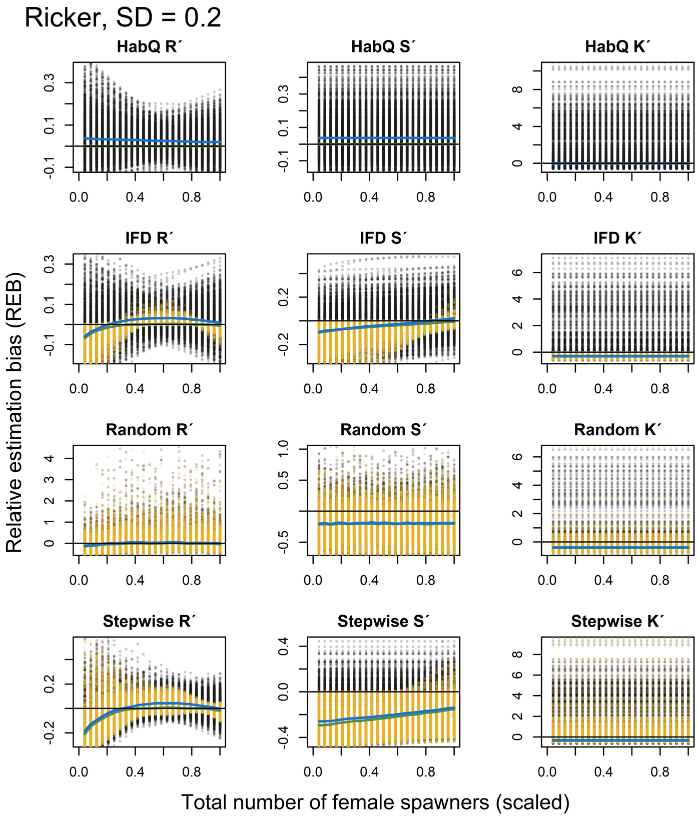


FIGURE 8 REB for R', S' and K', based on low spawner abundance ($K_{tot,j}/2$) without (yellow dots) and with added measurement error (SD = 0.2, black dots), for a Ricker SR relationship. Green and blue solid lines show the median REB without and with measurement error, respectively. Black solid line shows zero REB. Note the different scales on the Y-axis. For clearer visualization, female abundance (x-axis) is displayed as a proportion of the evaluated maximum abundance.

errors if the spawner behavior is either HabQ or IFD. In contrast, for both the Beverton-Holt and Ricker functions, a stepwise or random spawner behavior may introduce additional uncertainties that are not explained by the measurement error (i.e. variation in the REB is higher than what is added by the measurement error) Measurement errors are most often accounted for in stock assessment (Brooks et al., 2019), but additional estimation bias might be introduced by the underlying spawner behavior. The majority of the REB in our analyses was negative, which means that the productivity was underestimated. Underestimation of population productivity may lead to underutilization of populations, whereas overestimation may tend to produce overly-optimistic management advice (Conn et al., 2010; Hilborn et al., 2015), ultimately also resulting in lost yield. The extent of the loss can depend on the magnitude of the bias. Our results show that the magnitude and direction (under−/overestimation) of the parameter estimation bias depends on the spawner behavior and varies over the population abundance range. This is mainly an effect of the under−/overutilization of local spawning sites depending on the spawner distribution pattern. Irregular productivity regimes, not only depending on abundance, have been raised as an important factor in fisheries management (Vert-pre et al., 2013). Our results suggest that the spawner behavior might be one component contributing to this irregularity in productivity and that the productivity can vary according to population density.

For habitat restoration, ignoring the underlying distribution patterns of spawners may directly affect the outcome of restoration objectives, since habitats could be over- or underutilized compared with the common SR assumption, where spawners would utilize all potential spawning sites instantly and distribute homogenously across all spawning sites. This could ultimately make predictions of a system's productivity biased. Notably, if spawners follow a stepwise pattern and distribute according to the recruitment migration distance and the local carrying capacity, colonization of new habitats would probably be delayed compared with a more homogeneous spawner distribution (Einum et al., 2008b; Huxel & Hastings, 1999). Moreover, our results show that productivity is not stationary over the spawner abundance range. Results based on global SR functions may thus deviate considerably from the actual SR relationship of the global population in certain population ranges, where under−/overestimations of the survival parameters depend on the distribution pattern. Therefore, for recovering exploited populations, knowledge of the underlying distribution pattern of reproducing individuals

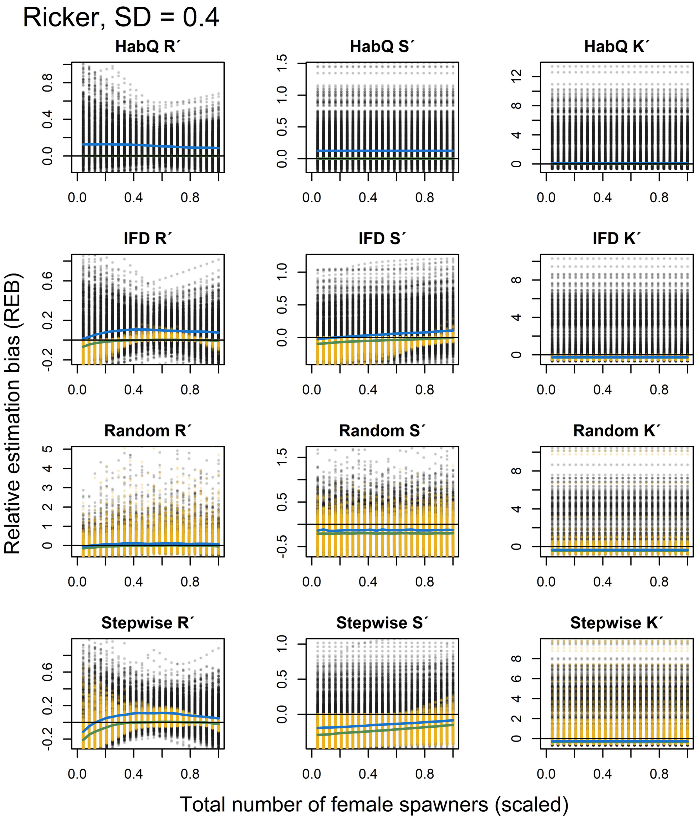


FIGURE 9 REB for R', S' and K', based on low spawner abundance ($K_{tot,j}/2$) without (yellow dots) and with added measurement error (SD = 0.4, black dots), for a Ricker SR relationship. Green and blue solid lines show the median REB without and with measurement error, respectively. Black solid line shows zero REB. Note the different scales on the Y-axis. For clearer visualization, female abundance (x-axis) is displayed as a proportion of the evaluated maximum abundance.

could be important for accurate stock-recruit parameter estimation and robust predictions of population development.

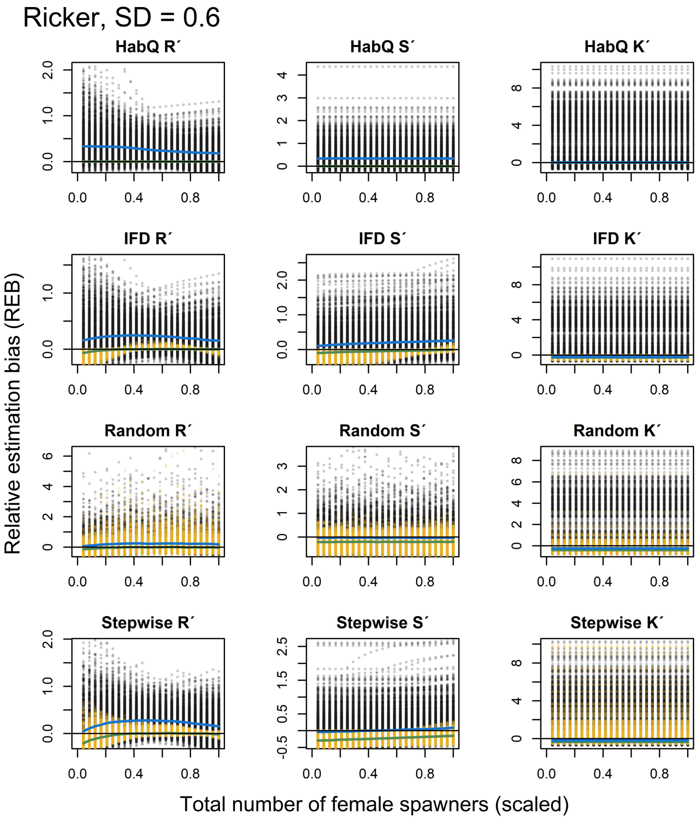
4.2 | Directions for future research

Spawner behaviors can be modeled and included in stock assessments; however, to do so, the specific behavior needs to be known, since the variability depends on the population (stock) specific spawner behavior. Empirical studies show that different fish species may display different distribution patterns (e.g. Foldvik et al., 2010; Huntsman et al., 2017; Langangen & Stige, 2021), indicating the lack of a general spawner distribution model that can be applied in stock assessments. It is beyond the scope of this study to provide a general suggestion on how to statistically handle spawner behavior patterns in stock assessments, but more stock-specific knowledge of spawner distribution appears warranted, which can be obtained for some species via e.g. telemetry studies (Dean et al., 2014) or nest counts (Finstad et al., 2013). As an extension to our present study, we are currently exploring if the spawner distribution behavior of Atlantic salmon could be detected using empirical spatio-temporal data on juvenile abundance (from electrofishing) together with spawner counts. This could be one way forward to gain more knowledge of the distribution behavior before additional data from other methods are available.

4.3 | Main conclusion

Using theoretically possible spawner distribution patterns, our results show that, when applying commonly used SR functions, the underlying distribution patterns of spawning individuals can affect estimates of SR parameters that govern the productivity of exploited fish stocks. Moreover, for stock assessments, the results from this simulation study suggest that any underlying distribution pattern that deviates from a homogenous distribution of spawning individuals can introduce systematic bias in parameter estimates, where the magnitude of estimation bias depends on the underlying spawning distribution pattern. For some of the spawner behaviors evaluated, realistic levels of measurement error (SD ≥ 0.2) would introduce larger bias than resulting from the spawner behavior, which makes measurement errors of higher concern from a management

FIGURE 10 REB for R', S' and K', based on low spawner abundance ($K_{tot,j}/2$) without (yellow dots) and with added measurement error (SD = 0.6, black dots), for a Ricker SR relationship. Green and blue solid lines show the median REB without and with measurement error, respectively. Black solid line shows zero REB. Note the different scales on the Y-axis. For clearer visualization, female abundance (x-axis) is displayed as a proportion of the evaluated maximum abundance.



perspective. Moreover, the majority of the estimation bias was of a precautionary nature (underestimation), which means that violating the spawner distribution assumption will not lead to unsustainable harvest rates but rather a potential loss of yield. To reduce potential estimation bias, further research into stock-specific spawner distribution patterns is needed.

AUTHOR CONTRIBUTIONS

Stefan Skoglund: Formal analysis (lead); methodology (equal); validation (lead); visualization (lead); writing – original draft (lead); writing – review and editing (lead). **Rebecca Whitlock:** Conceptualization (equal); formal analysis (equal); methodology (equal); supervision (equal); validation (equal); visualization (equal); writing – review and editing (equal). **Erik Petersson:** Supervision (equal); writing – review and editing (equal). **Stefan Palm:** Conceptualization (equal); supervision (equal); validation (equal); writing – review and editing (equal). **Kjell Leonardsson:** Conceptualization (equal); methodology (equal); supervision (equal); validation (equal); visualization (equal); writing – review and editing (equal).

ACKNOWLEDGMENTS

We thank Josefin Sundin and three anonymous reviewers for comments that have improved the manuscript.

FUNDING INFORMATION

The project is funded by the Swedish University of Agricultural Science, without any funding ID-number.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in figshare at https://figshare.com/account/home#/projects/154619, reference number 154619.

ORCID

Stefan Skoglund https://orcid.org/0000-0003-3110-2854

REFERENCES

Abesamis, R. A., & Russ, G. R. (2005). Density-dependent spillover from a marine reserve: Long-term evidence. *Ecological Applications*, *15*, 1798–1812.

Bartolino, V., Ciannelli, L., Bacheler, N. M., & Chan, K. S. (2011). Ontogenetic and sex-specific differences in density-dependent habitat selection of a marine fish population. *Ecology*, *92*, 189–200.

Beverton, R. J. H., & Holt, S. J. (1957). *On the dynamics of exploited fish populations*. Ministry of Agriculture, Fisheries and Food, London.

Bietz, B. F. (1981). Habitat availability, social attraction and nest distribution patterns in longear sunfish (*Lepomis megalotis* peltastes). *Environmental Biology of Fishes*, *6*, 193–200.

Bouchard, C., Bardonnet, A., Buoro, M., & Tentelier, C. (2018). Effects of spatial aggregation of nests on population recruitment: The case of a small population of Atlantic salmon. *Ecosphere*, *9*, e02178.

Brooks, E. N., & Powers, J. E. (2007). Generalized compensation in stock-recruit functions: Properties and implications for management. *ICES Journal of Marine Science*, *64*, 413–424.

Brooks, E. N., Thorson, J. T., Shertzer, K. W., Nash, R. D. M., Brodziak, J. K. T., Johnson, K. F., Klibansky, N., Wells, B. K., & White, J. (2019). Paulik revisited: Statistical framework and estimation performance of multistage recruitment functions. *Fisheries Research*, *217*, 58–70.

Ciannelli, L., Neuheimer, A. B., Stige, L. C., Frank, K. T., Durant, J. M., Hunsicker, M., Rogers, L. A., Porter, S., Ottersen, G., & Yaragina, N. A. (2022). Ontogenetic spatial constraints of sub-arctic marine fish species. *Fish and Fisheries*, *23*, 342–357.

Conn, P. B., Williams, E. H., & Shertzer, K. W. (2010). When can we reliably estimate the productivity of fish stocks? *Canadian Journal of Fisheries and Aquatic Sciences*, *67*, 511–523.

Cram, J. M., Torgersen, C. E., Klett, R. S., Pess, G. R., May, D., Pearsons, T. N., & Dittman, A. H. (2013). Tradeoffs between homing and habitat quality for spawning site selection by hatchery-origin Chinook salmon. *Environmental Biology of Fishes*, *96*, 109–122.

Dean, M. J., Hoffman, W. S., Zemeckis, D. R., & Armstrong, M. P. (2014). Fine-scale diel and gender-based patterns in behaviour of Atlantic cod (*Gadus morhua*) on a spawning ground in the Western gulf of Maine. *ICES Journal of Marine Science*, *71*, 1474–1489.

Dingsør, G. E., Ciannelli, L., Chan, K. S., Ottersen, G., & Stenseth, N. C. (2007). Density dependence and density Independence during the early life stages of four marine fish stocks. *Ecology*, *88*, 625–634.

Einum, S., & Nislow, K. H. (2005). Local-scale density-dependent survival of mobile organisms in continuous habitats: An experimental test using Atlantic salmon. *Oecologia*, *143*, 203–210.

Einum, S., Nislow, K. H., Mckelvey, S., & Armstrong, J. D. (2008). Nest distribution shaping within-stream variation in Atlantic salmon juvenile abundance and competition over small spatial scales. *The Journal of Animal Ecology*, *77*, 167–172.

Einum, S., Nislow, K. H., Reynolds, J. D., & Sutherland, W. J. (2008). Predicting population responses to restoration of breeding habitat in Atlantic salmon. *Journal of Applied Ecology*, *45*, 930–938.

Falcy, M. R. (2015). Density-dependent habitat selection of spawning Chinook salmon: Broad-scale evidence and implications. *The Journal of Animal Ecology*, *84*, 545–553.

Feiner, Z. S., Bunnell, D. B., Höök, T. O., Madenjian, C. P., Warner, D. M., & Collingsworth, P. D. (2015). Non-stationary recruitment dynamics of rainbow smelt: The influence of environmental variables and variation in size structure and length-at-maturation. *Journal of Great Lakes Research*, *41*, 246–258.

Fernández-Bellon, D., Cortés-Avizanda, A., Arenas, R., & Donázar, J. A. (2016). Density-dependent productivity in a colonial vulture at two spatial scales. *Ecology*, *97*, 406–416.

Finstad, A. G., Einum, S., Ugedal, O., & Forseth, T. (2009). Spatial distribution of limited resources and local density regulation in juvenile Atlantic salmon. *The Journal of Animal Ecology*, *78*, 226–235.

Finstad, A. G., Sættem, L. M., & Einum, S. (2013). Historical abundance and spatial distributions of spawners determine juvenile habitat accessibility in salmon: Implications for population dynamics and management targets. *Canadian Journal of Fisheries and Aquatic Sciences*, *70*, 1339–1345.

Fleming, I. A. (1996). Reproductive strategies of Atlantic salmon: Ecology and evolution. *Reviews in Fish Biology and Fisheries*, *6*, 379–416.

Foldvik, A., Finstad, A. G., & Einum, S. (2010). Relating juvenile spatial distribution to breeding patterns in anadromous salmonid populations. *The Journal of Animal Ecology*, *79*, 501–509.

Foss-Grant, A. P., Zipkin, E. F., Thorson, J. T., Jensen, O. P., & Fagan, W. F. (2016). Hierarchical analysis of taxonomic variation in intraspecific competition across fish species. *Ecology*, *97*, 1724–1734.

Fretwell, S. D., & Lucas, H. L. (1970). On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoretica*, *19*, 16–36.

Gilbert, D. J. (1997). Towards a new recruitment paradigm for fish stocks. *Journal of Fisheries and Aquatic Science*, *54*, 969–977.

Green, B. S. (2008). Chapter 1 maternal effects in fish populations. In D. W. Sims (Ed.), *Advances in marine biology* (pp. 1–105). Academic Press.

Haddon, M. (2001). *Modelling and quantitative methods in fisheries*. Chapman & Hall/CRC.

Haugen, T. O., Winfield, I. J., Vøllestad, L. A., Fletcher, J. M., James, J. B., & Stenseth, N. C. (2006). The ideal free pike: 50 years of fitness-maximizing dispersal in Windermere. *Proceedings of the Biological Sciences*, *273*, 2917–2924.

Hilborn, R., Fulton, E. A., Green, B. S., Hartmann, K., Tracey, S. R., & Watson, R. A. (2015). When is a fishery sustainable? *Journal of Fisheries and Aquatic Science*, *72*, 1433–1441.

Hilborn, R., & Walters, C. J. (2015). *Quantitative fisheries stock assessment: Choice, dynamics and uncertainty*. Springer.

Holt, C. A., & Michielsens, C. G. J. (2020). Impact of time-varying productivity on estimated stock–recruitment parameters and biological reference points. *Journal of Fisheries and Aquatic Science*, *77*, 836–847.

Huntsman, B. M., Falke, J. A., Savereide, J. W., & Bennett, K. E. (2017). The role of density-dependent and –independent processes in spawning habitat selection by salmon in an Arctic riverscape. *PLoS One*, *12*, e0177467.

Huxel, G. R., & Hastings, A. (1999). Habitat loss, fragmentation, and restoration. *Restoration Ecology*, *7*, 309–315.

Jonzen, N., Wilcox, C., & Possingham, H. P. (2004). Habitat selection and population regulation in temporally fluctuating environments. *The American Naturalist*, *164*, E103–E114.

Kapur, M. S., Siple, M. C., Olmos, M., Privitera-Johnson, K. M., Adams, G., Best, J., Castillo-Jordán, C., Cronin-Fine, L., Havron, A. M., Lee, Q., Methot, R. D., & Punt, A. E. (2021). Equilibrium reference point calculations for the next generation of spatial assessments. *Fisheries Research*, *244*, 106132.

Langangen, O., & Stige, L. C. (2021). Shedding light on the link between the spatial distribution of eggs and survival in Northeast Arctic cod. *Fisheries Oceanography*, *30*, 429–436.

Lee, H.-H., Maunder, M. N., Piner, K. R., & Methot, R. D. (2012). Can steepness of the stock–recruitment relationship be estimated in fishery stock assessment models? *Fisheries Research*, *125–126*, 254–261.

Levin, S. A. (1992). The problem of pattern and scale in ecology: The Robert H. MacArthur award lecture. *Ecology*, *73*, 1943–1967.

Linton, B. C., & Bence, J. R. (2008). Evaluating methods for estimating process and observation error variances in statistical catch-at-age analysis. *Fisheries Research*, *94*, 26–35.

Lowerre-Barbieri, S., DeCelles, G., Pepin, P., Catalán, I. A., Muhling, B., Erisman, B., Cadrin, S. X., Alós, J., Ospina-Alvarez, A., Stachura, M. M., Tringali, M. D., Burnsed, S. W., & Paris, C. B. (2017). Reproductive resilience: A paradigm shift in understanding spawner-recruit systems in exploited marine fish. *Fish and Fisheries*, *18*, 285–312.

MacCall, A. D., Francis, T. B., Punt, A. E., Siple, M. C., Armitage, D. R., Cleary, J. S., Dressel, S. C., Jones, R. R., Kitka, H., Lee, L. C., Levin, P. S., McIsaac, J., Okamoto, D. K., Poe, M., Reifenstuhl, S., Schmidt, J. O., Shelton, A. O., Silver, J. J., Thornton, T. F., … Woodruff, J. (2019).

A heuristic model of socially learned migration behaviour exhibits distinctive spatial and reproductive dynamics. *ICES Journal of Marine Science*, *76*, 598–608.

Maunder, M. N., & Deriso, R. B. (2013). A stock–recruitment model for highly fecund species based on temporal and spatial extent of spawning. *Fisheries Research*, *146*, 96–101.

Maunder, M. N., & Piner, K. R. (2015). Contemporary fisheries stock assessment: Many issues still remain. *ICES Journal of Marine Science*, *72*, 7–18.

Mayor, S. J., Schneider, D. C., Schaefer, J. A., & Mahoney, S. P. (2009). Habitat selection at multiple scales. *Écoscience*, *16*, 238–247.

Memarzadeh, M., Britten, G. L., Worm, B., & Boettiger, C. (2019). Rebuilding global fisheries under uncertainty. *Proceedings of the National Academy of Sciences*, *116*, 15985–15990.

Morris, D. W. (1987). Tests of density-dependent habitat selection in a patchy environment. *Ecology Monograph*, *57*, 270–281.

Myers, R. A. (2001). Stock and recruitment: Generalizations about maximum reproductive rate, density dependence, and variability using meta-analytic approaches. *ICES Journal of Marine Science*, *58*, 937–951.

Myers, R. A., & Barrowman, N. J. (1996). Is fish recruitment related to spawner abundance. *Fishery Bulletin*, *94*, 707–724.

Needle, C. L. (2002). Recruitment models: diagnosis and prognosis. *Reviews in Fish Biology and Fisheries*, *11*, 95–111.

Padfield, D., & Matheson, G. (2018). Nls. Multstart: Robust non-linear regression using AIC scores. R Package Version.

Pulkkinen, H., & Mäntyniemi, S. (2013). Maximum survival of eggs as the key parameter of stock–recruit meta-analysis: Accounting for parameter and structural uncertainty. *Journal of Fisheries and Aquatic Science*, *70*, 527–533.

Pulliam, H. R., & Danielson, B. J. (1991). Sources, sinks, and habitat selection: A landscape perspective on population dynamics. *The American Naturalist*, *137*, S50–S66.

Purchase, C. F., & Hutchings, J. A. (2008). A temporally stable spatial pattern in the spawner density of a freshwater fish: Evidence for an ideal despotic distribution. *Journal of Fisheries and Aquatic Science*, *65*, 382–388.

Quinn, T. J., & Deriso, R. B. (1999). *Quantitative fish dynamics*. Oxford University Press.

R Core Team. (2022). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing.

Ray, C., & Hastings, A. (1996). Density dependence: Are we searching at the wrong spatial scale? *The Journal of Animal Ecology*, *65*, 556–566.

Ricker, W. E. (1954). Stock and recruitment. *Journal of the Fisheries Research Board of Canada*, *11*, 559–623.

Rogers, L. A., Storvik, G. O., Knutsen, H., Olsen, E. M., & Stenseth, N. C. (2017). Fine-scale population dynamics in a marine fish species inferred from dynamic state-space models. *The Journal of Animal Ecology*, *86*, 888–898.

Shelton, A. O., Munch, S. B., Keith, D., & Mangel, M. (2012). Maternal age, fecundity, egg quality, and recruitment: Linking stock structure to recruitment using an age-structured Ricker model. *Journal of Fisheries and Aquatic Science*, *69*, 1631–1641.

Shepherd, T. D., & Litvak, M. K. (2004). Density-dependent habitat selection and the ideal free distribution in marine fish spatial dynamics: Considerations and cautions. *Fish and Fisheries*, *5*, 141–152.

Sinclair, A. R. E., & Pech, R. P. (1996). Density dependence, Stochasticity, compensation and predator regulation. *Oikos*, *75*, 164–173.

Skjæraasen, J. E., Meager, J. J., Karlsen, Ø., Hutchings, J. A., & Ferno, A. (2011). Extreme spawning-site fidelity in Atlantic cod. *ICES Journal of Marine Science*, *68*, 1472–1477.

Taylor, I. G., Gertseva, V., Methot, R. D., & Maunder, M. N. (2013). A stock–recruitment relationship based on pre-recruit survival, illustrated with application to spiny dogfish shark. *Fisheries Research*, *142*, 15–21.

Teichert, M. A. K., Foldvik, A., Forseth, T., Ugedal, O., Einum, S., Finstad, A. G., Hedger, R. D., & Bellier, E. (2010). Effects of spawning distribution on juvenile Atlantic salmon (Salmo salar) density and growth. *Journal of Fisheries and Aquatic Science*, *68*, 43–50.

Thorson, J. T., Jensen, O. P., & Zipkin, E. F. (2014). How variable is recruitment for exploited marine fishes? A hierarchical model for testing life history theory. *Journal of Fisheries and Aquatic Science*, *71*, 973–983.

Thorson, J. T., Rindorf, A., Gao, J., Hanselman, D. H., & Winker, H. (2016). Density-dependent changes in effective area occupied for sea-bottom-associated marine fishes. *Proceedings of the Royal Society B: Biological Sciences*, *283*, 20161853.

Turchin, P. (1999). Population regulation: A synthetic view. *Oikos*, *84*, 153–159.

Vert-pre, K. A., Amoroso, R. O., Jensen, O. P., & Hilborn, R. (2013). Frequency and intensity of productivity regime shifts in marine fish stocks. *Proceedings of the National Academy of Sciences*, *110*, 1779–1784.

Walters, C. J. (1985). Bias in the estimation of functional relationships from time series data. *Journal of Fisheries and Aquatic Science*, *42*, 147–149.

Walters, C. J., & Ludwig, D. (1981). Effects of measurement errors on the assessment of stock–recruitment relationships. *Canadian Journal of Fisheries and Aquatic Sciences*, *38*, 704–710.

Walters, C. J., & Martell, S. J. D. (2004). *Fisheries ecology and management*. Princeton University Press.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Skoglund, S., Whitlock, R., Petersson, E., Palm, S., & Leonardsson, K. (2022). From spawner habitat selection to stock-recruitment: Implications for assessment. *Ecology and Evolution*, *12*, e9679. https://doi.org/10.1002/ece3.9679

Supplementary Information (SI)

Here is the derivations proving that the Beverton-Holt SR function (valid also for Ricker)

s = density independent survival during the juvenile phase, e.g. in the river. Here assumed to be the same for all spawning grounds.

$N = \sum_{i=1}^{\max} n_i$, (spawners and their fecundity)

$K = \sum_{i=1}^{\max} k_i$, (carrying capacities)

The proof below is for the Beverton-Holt SR function, but the same method can be used to verify that it holds also for the Ricker SR function.

Show that the left-hand side (LHS) equals the right-hand side (RHS) of the two alternative formulations of Beverton-Holt functions below, which both aggregate spawners (n_i) from an arbitrary number (max) of spawning grounds each with its unique carrying capacities $k_{i,\, i=1\text{-}\max}$. The LHS version sums the BH functions (local recruitment) from each local spawning ground, while the RHS version is a single traditional BH function that directly calculates the total recruitment by using the total number of spawners as well as the total carrying capacity.

$\sum_{i=1}^{\max}(s * n_i/(1 + s * n_i/k_i)) = s * \sum_{i=1}^{\max} n_i/(1 + s * \sum_{i=1}^{\max} n_i/\sum_{i=1}^{\max} k_i)$

Substitute $\sum_{i=1}^{\max} n_i$ with N, and $\sum_{i=1}^{\max} k_i$ with K into the RHS

$\sum_{i=1}^{\max}(s * n_i/(1 + s * n_i/k_i)) = s * N/(1 + s * N/K)$

Assume that the spawners select spawning grounds directly proportional to the carrying capacities of the spawning grounds (habQ scenario).

This means that for example $n_i = N * k_i/K$ spawners will select spawning ground i.

Replace n_i with $N * k_i/K$ in the LHS.

$\sum_{i=1}^{\max}(s\, N\, k_i/K/(1 + s * N\, k_i/K/k_i)) = s * N/(1 + s * N/K)$

Simplify

$s * N/K * (\sum_{i=1}^{\max} k_i)/(1 + s * N/K) = s * N/(1 + s * N/K)$

Replace $\sum_{i=1}^{\max} k_i$ with K

$s * N/K * K/(1 + s * N/K) = s * N/(1 + s * N/K)$

Simplifying after the last substitution gives LHS=RHS

$s * N/(1 + s * N/K) = s * N/(1 + s * N/K)$

Conclusion

The two alternative formulations of the Beverton-Holt function are identical given the assumptions made. Following the description above it turns out that it is valid also for the Ricker function. Hence, the traditional Beverton-Holt as well as the Ricker stock recruitment functions allow for heterogenous recruitment areas (varying size or quality) when the spawners choose the spawning grounds in proportion to the size or quality of the available spawning grounds and when the density independent survival of the offspring is the same in each area. In fact, there is some possibility for varying density independent offspring survival, but that requires $s0_i*s1_i=s0_j*s1_j$ for all i and j. Moreover, as the total spawner density increase the influence of the density independent survival parameters decreases, implying that the LHS and the RHS of the above expression will be fairly equal even when there are some deviation in density independent survival between the areas, as can be seen in the habQ graphs showing a small bias of the global Beverton-Holt and Ricker SR-functions at increasing female numbers.

ACTA UNIVERSITATIS AGRICULTURAE SUECIAE

DOCTORAL THESIS NO. 2024:18

In fisheries ecology population regulation is the foundation that allows sustainable harvest of natural populations. This thesis explore potential sources of bias in stock recruitment relationships in Atlantic salmon (*Salmo salar*) in the Baltic Sea. Spawning behaviours are evaluated and alternative methods investigated that can be used in order to improve estimates in stock-assessments. In addition experiments revealed that juveniles of Atlantic salmon and brown trout (*Salmo trutta*) outcompete each other and this relationship is not density-dependent but rather temperature-dependent.

Stefan Skoglund got his undergraduate education, and received his Bachelor degree in Marine biology and his Master degree in Marine biology at Stockholm University.

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

SLU generates knowledge for the sustainable use of biological natural resources. Research, education, extension, as well as environmental monitoring and assessment are used to achieve this goal.

ISSN 1652-6880
ISBN (print version) 978-91-8046-300-3
ISBN (electronic version) 978-91-8046-301-0