

# TEMPORAL AND DENSITY-DEPENDENT VARIABILITY AS SOURCE FOR UNCERTAINTY IN FISH POPULATION DYNAMICS

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ACADEMIC DISSERTATION

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*Earth is abundant with plentiful resources. Our practice of rationing resources through monetary control is no longer relevant and is counter-productive to our survival.*

*Jacque Fresco*

# ABSTRACT

Considering the uncertainties about model parameters and structure, observations, and the resulting predictions is crucial when managing natural resources. This thesis is compiled of four research articles that deal with uncertainties and change in marine fish populations. In all the articles, the Bayesian statistical modelling framework is adopted to account for various types of uncertainty. When modelling complex systems, one must recognize that all models are only approximations of reality and are based on the limited understanding about the system at that moment and on previously observed behaviour. Even if a model explains the recent behaviour and predicts how the system will respond in the near future, there is always a possibility that the system changes thus rendering the old model useless. Approaches to respond to sudden changes in the system's dynamics are vital for successful resource management.

Fish populations' renewal ability is mainly determined by their reproductive success. Thus, it is of utmost importance to be able to understand and model the reproductive dynamics of marine fish populations. In this thesis, fish reproduction is studied using models that link together the number of new individuals entering the adult population (recruits) and the size of the reproducing component of the population (spawning stock), namely, the stock-recruitment relationship. The focus in this work is on temporal and density-dependent variability in the stock-recruitment relationship.

The temporal variability is studied using Bayesian change-point detection methods applied to detecting changes in the per capita reproductive output of four Atlantic cod populations by analysing recruit-per-spawner ratios, and in the parameters of the stock-recruitment relationship of four fish species in the southern Gulf of St. Lawrence. In this work, novel Bayesian methods are utilized to improve the handling of uncertainties about the parameters, the timings of the changes, and in short term predictions. This thesis presents computational methods for analysing temporal variability in linear-Gaussian problems where analytical solutions are available, and extend the methodology to analytically intractable non-linear and non-Gaussian problems by utilizing numerical approximate solutions.

Traditionally, compensatory population dynamics have been assumed in marine fish populations. The validity of the assumption of compensatory stock-recruitment relationship is examined by studying the density-dependence of nine Atlantic herring populations at low population sizes using models that better capture the uncertainty related to low-abundance dynamics and allow for depensatory dynamics caused by Allee effects. The Allee effect

has been largely ignored in marine fish population models. Here methodology for detecting Allee effects is developed, and it is concluded that Allee effects might be more common than previously thought.

In Bayesian models, expert elicitation is used to construct prior distributions for the model parameters. When observational data is scarce or not available, informative prior distributions are crucial for conducting inference. However, experts might not be calibrated and can have significant biases in their assessments about key parameters of the models. Statistical models are developed for the use of miscalibration data to infer and to correct for experts' biases in their assessments.

# LIST OF ARTICLES

This thesis consists of a summary part and four research articles. The articles that are published have been reproduced with the permission of the journals concerned.

- I. Perälä T. and Kuparinen A. 2015. Detecting regime shifts in fish stock dynamics. *Canadian Journal of Fisheries and Aquatic Sciences*. 72(11): 1619-1628.
- II. Perälä T. A., Swain D. P., and Kuparinen A. 2016. Examining nonstationarity in the recruitment dynamics of fishes using Bayesian change point analysis. *Canadian Journal of Fisheries and Aquatic Sciences*. 74(5): 751-765.
- III. Perälä T. and Kuparinen A. 2017. Detection of Allee effects in marine fishes: analytical biases generated by data availability and model selection. *Proceedings of the Royal Society B series*. 284(1861)
- IV. Perälä T., Chrysafi A. and Vanhatalo J. Expert calibration with hierarchical Gaussian process models. *Bayesian Analysis*. (submitted).

The articles are referred to in the text by their roman numerals.



# THE INDIVIDUAL CONTRIBUTIONS OF THE AUTHORS OF ARTICLES I-IV

- I. Tommi Perälä had the main responsibility in conducting the literature review, choosing the data, formulating the model, programming the algorithm for and conducting the inference, testing the model and the algorithm in simulation setting, and writing the article. Anna Kuparinen provided the simulated data and assisted in writing the article.
- II. Tommi Perälä had the main responsibility in conducting the literature review, formulating the model, programming the algorithm for and conducting the inference, testing the model and the algorithm in simulation setting, and writing the article. Douglas Swain assisted in choosing the data, providing help with the literature review, analysing the results and writing the article. Anna Kuparinen assisted in writing the article.
- III. Tommi Perälä had the main responsibility in formulating the models and conducting the inference. The article was written jointly by Tommi Perälä and Anna Kuparinen.
- IV. Tommi Perälä had the main responsibility of formulating the models, carrying out the inference, and testing the models in simulation setting. Anna Chrysafi provided the data elicited from experts and the original idea. The article was written jointly by Tommi Perälä, Jarno Vanhatalo and Anna Chrysafi.

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# 1 INTRODUCTION

It has been shown time and time again how short-sighted approaches for short-term profit maximization have led to over exploitation of the resources or even to full scale destruction of vital life supporting ecosystems. While the motivation behind these primitive unsustainable strategies will likely not change without a full-scale redesign of our culture and socioeconomic systems, science keeps providing better understanding of the natural processes and better tools to handle the unknown and the unexpected.

For the better part of the history of human exploitation of marine fishes, the marine fish resources were considered infinite. This ignorant mindset is well apparent in the infamous 1883 quote by T. H. Huxley stating: "I believe, then, that the cod fishery... and probably all the great sea fisheries, are inexhaustible: that is to say that nothing we do seriously affects the number of fish. And any attempt to regulate these fisheries seems... to be useless.". However, with rapidly growing demand for protein for the growing human population together with the development of more efficient fishing technologies, the limits for the exploitation of this precious finite resource started to show.

Alarming global trends have emerged. Despite the increase in fishing efficiency and effort, the total catch of marine fish has declined by roughly 10% per year during the period 1988-2000 (Watson and Pauly 2001). Also, in the 2014 report on the state of the world fisheries and aquaculture, the United Nations Food and Agricultural Organization (FAO) estimated that approximately 57% of the world's fish stocks are fully exploited and 30% are over-exploited, depleted or recovering (FAO 2014).

Considering the dire situation, there is an urgent need for sustainable fishing practices and science-based fish stock management. One conception of sustainable fishing is to operate at a dynamic equilibrium so that the fish population can renew itself at the same pace as the fish are removed by fishing (Hilborn 2005). Moreover, for maximal efficiency, that is, to obtain as much fish for human consumption as possible, the fish stocks should be managed so that they settle at a dynamic equilibrium, which produces the maximum sustainable yield. From the conservation point of view, sustainability might even mean that the whole ecosystem should recover to a pristine condition. To accomplish any of these goals, good knowledge about the current state and the dynamics of the fish populations are required.

## **FISH POPULATION DYNAMICS**

The dynamics of marine fish populations are particularly challenging to study because it is impossible to observe the state of the fish populations directly.

Thus, stock assessments that utilize complex population dynamic models combined with biological and fisheries data are conducted regularly to inform fisheries management about the state of the worlds fisheries.

Fish population dynamics models consists of several sub-models that describe different processes related to the dynamics of the population. Although population dynamics models differ in structure and resolution, all of them include mechanistic descriptions for the growth, survival and reproduction of the fish. Inference of the model parameters and state variables is carried out via observation models that link the fishery data to the model variables.

### **ACKNOWLEDGING UNCERTAINTY**

Another great challenge for fisheries is that they are full of uncertainties. These uncertainties stem from different sources and can be seen to represent different types of uncertainties. Categorizing these uncertainties is a challenging task, and many authors have tried to find meaningful and useful categories (see for example Charles (1998) and Kennedy and O'Hagan (2001)).

Proper accounting for of all the uncertainties related to fisheries is crucial for management to arrive at correct decisions when setting fishery policy. Fisheries are expected to follow the precautionary approach, which states that when there is a risk related to an action, it should not be executed until it can be scientifically proven to be safe. Historically fisheries managers have operated conversely by acting first, and only after an action has already been proven to have caused damage, refraining from repeating the action (Dayton 1998). Nowadays, the precautionary approach is enforced by legislation at least in Europe (EC 2000) and the US (USC 1996).

Bayesian inference provides a formal methodological framework to uncertainty modelling, and its benefits in fisheries stock assessment and decision making have been recognized (Punt and Hilborn 1997, McAllister and Kirkwood 1998, Meyer and Millar 1999, Hilborn 2003). Bayesian statistics is essentially a method for formulating subjective beliefs about the state of nature as probability statements, and updating these beliefs with evidence using the laws of probability calculus.

In this work the Bayesian statistical framework for uncertainty modelling is adopted. The author's view on uncertainties is, that uncertainty is always subjective, and it is important to clarify whose uncertainty the models are describing. This is in line with the Bayesian philosophy. In this work, the modeller's uncertainty about the structure of the models is one main theme. Another important part of this work is describing the uncertainties about the model parameters. A less commonly discussed form of uncertainty also touched upon in this work is the modeller's uncertainty about a subject, when all the information the modeller has about it is other people's subjective statements. The challenge, then, is how to formally formulate the modeller's uncertainty by combining the subjective beliefs of these people.

## **THE IMPORTANCE OF REPRODUCTION**

Reproduction is often regarded as the most important factor affecting the fish populations' renewal ability and resilience to fishing, and is thus of great interest to fisheries scientists (Hilborn and Walters 1992). The quest for understanding fish reproduction has been mainly focused on finding mathematical models that describe the so-called stock-recruitment (S-R) relationship that describe the link between the reproducing component of the population (spawning stock, S) and the juveniles produced by the spawning stock entering the population (recruits, R) (Hilborn and Walters 1992). Understanding this relationship is essential for fish stock management, since it is used for determining catch quotas, setting biological reference points, estimating stock extinction probabilities and how the fish stock will react to different fishing strategies (Myers 2001, Myers et al. 2001).

The prevalent approach to S-R modelling has been based on the theory of compensatory population dynamics, which assumes that populations grow at fastest rates at very low abundances where intra-specific competition is considered negligible. As the size of the population increases, the number of recruits per spawner decreases because of density dependent effects such as increased competition on available food resources, predation and easier spread of diseases. As the population size increases even further some species may even resort to cannibalism, which might result in further decrease in recruitment. The models are then fitted to all available historical data, and used to predict the future recruitment.

In contrast to compensatory population dynamics, depensatory population dynamics assume that at sufficiently low abundances the per capita population growth rate decreases as the population abundance decreases. This phenomenon is called the Allee effect (Stephensen et al. 1999, Hutchings 2015). For example, the difficulty in finding mates in a sparse population can be one of the factors hindering the population growth (Stephensen et al. 1999).

In marine fisheries, the Allee effects have been mostly ignored since studies on marine fishes have not been able to detect them (e.g. Myers et al. 1995, Liermann and Hilborn 1997, Hilborn et al. 2014). However, these studies have been criticized for having too little data at low abundances to be able to draw any conclusions about the presence of Allee effects (Hutchings 2015).

The population's ability to grow at low abundances is crucial for its recovery potential, resilience to environmental and anthropogenic alterations, and to minimize its risk of extinction (Dulvy et al. 2004, Mace et al. 2008). Humans tend to over-exploit natural resources, and thus, it is paramount to understand how the marine fish populations might respond if their abundance is dramatically reduced.

## **THE EFFECTS OF CHANGING ENVIRONMENT**

There is ample evidence that marine ecosystems can experience dramatic changes where the whole system goes from one relatively stable state to

another (deYoung et al. 2008; Vasilakopoulos and Marshall 2015). In marine sciences these changes are often called regime shifts (Holbrook et al. 1997, Peterson and Schwing 2003, deYoung et al. 2004). These regime shifts are usually defined as sudden changes between alternate and persistent ecosystem states that involve multiple variables and wide spatial scales (de Young et al. 2008; Jiao 2009; Möllmann et al. 2015). They are the result of some internal processes or external forcing that drive the system over a tipping point thus altering the qualitative behaviour of the system.

The main driver of marine ecosystem regime shifts is the change in environmental conditions, mainly in the climate (Beamish et al. 2004, Jiao 2009). However, fishing has also been recognized as an important driver of marine ecosystem regime shifts (Möllmann et al. 2008; Jiao 2009). For example, a regime shift in the composition of the marine fish community in the southern Gulf of St. Lawrence has been attributed to the direct and indirect effects of fishing (Savenkoff et al. 2007, Benoît and Swain 2008).

Regime shifts can affect marine ecosystems by changing the species composition and the dynamics of the fish populations. For example, in the late 1980s, the central Baltic Sea regime shift decreased recruitment of Atlantic cod (*Gadus morhua*) which via decreased predation by cod on sprat (*Sprattus sprattus*) contributed to exceptional growth in sprat abundance (Alheit et al. 2005).

These shifts can manifest as changes in the recruitment dynamics of fish, which may alter the fish stock's resilience to fishing and its ability to recover from overfishing and stock collapse. Drivers of shifts in recruitment include changes in natural mortality and growth (Chouinard et al. 2006), size-selective fishing induced genetic changes in growth (Swain et al. 2007), changes in water temperature directly (Beaugrand 2004; O'Brien et al. 2000; Brunel and Boucher 2007) or indirectly because of declining size-at-age (Mohn and Chouinard 2004; Dutil et al. 1999), and fluctuations in plankton abundance (Beaugrand et al. 2003, Olsen et al. 2011).

It is thus paramount that the fisheries management can detect and adjust to shifts in recruitment dynamics, as failure to respond to the decrease in recruitment can lead to overexploitation and even to collapse of the fish stock. Such failure is believed to be the cause of the collapse of the Newfoundland cod fishery in Canada in the early 1990s, which caused considerable socio-economic costs to the local communities (Biggs et al. 2009).

Models incorporating or studying regime shifts in fish stock dynamics have been used before (Vert-pre et al. 2013, Wayte 2013, Munch and Kottas 2009, Ottersen et al. 2013). Vert-pre et al. (2013) studied 230 fish stocks and concluded that 69.1% of the stocks were best explained by a model that allowed for regime shifts (Vert-pre et al. 2013). Also, Ottersen et al. (2013) found that 27 out of the 38 North Atlantic stocks were better explained by a model allowing for shifts (Ottersen et al. 2013).

However, most of the studies have used frequentist methods, namely a sequential Student's t-test (STARS; Rodionov 2004) to detect shifts in the

mean level of a time-series. The method has severe limitations, since it does not include uncertainty in the timings of the shifts, nor can it be used for more complex models, and as it only detects shifts in the mean of the time-series, it does not detect changes in the variance, which might be equally important (Kuparinen et al. 2014).

Maximum likelihood based methods that are somewhat more flexible, since they can detect changes in both the mean and the variance of a time series, have also been used for shift detection in environmental monitoring (Liu 2010). They have also been successfully applied to fitting S-R models so that one stepwise change in the model parameters is allowed (Ottersen et al. 2013). These methods also omit uncertainty about the model parameters and the timing of the change.

Until now, the use of Bayesian methods in regime shift modelling has been very limited, and has focused on fitting a two-regime Ricker S-R model using Markov switching regression (Munch and Kottas 2009), which assumes that the recruitment randomly changes between two alternative states. The assumption of two reoccurring regimes might be adequate for some fish populations (e.g. Pacific mackerel (*Scomber japonicus*) fishery; Parrish and MacCall 1978), but such assumption is not necessarily valid for “real” systems (Steele 1996), particularly when there is an interplay between fishery and climate impacts (Jiao 2009).

## **EXPERT ELICITATION**

Traditional approaches to fisheries stock assessment require large amounts of fishery dependent and independent data (Magnusson and Hilborn 2007, Methot and Wetzel 2013), which makes their use difficult in situations where data is limited or lacking completely. Expert elicitation is an important part of decision making (O’Hagan et al. 2006), and it can be used to support statistical analyses when data is limited (Burgman 2005, Roman et al. 2008, Zickfeld et al. 2010) or when data collection is too costly or time consuming (Burgman et al. 2011, Morgan 2014). In Bayesian statistics, expert knowledge about the model parameters is formulated into informative prior distributions (Garthwaite et al. 2005, Uusitalo et al. 2005).

Expert elicitation has its problems, however, as experts have psychological biases, and these biases, if not accounted for, can significantly affect the model parameter inference and predictions. Experts may have biases in their parameter estimates, and they may also severely underestimate their own uncertainty about the parameters. If these biases are systematic, they can be inferred from calibration data using statistical models, and the experts’ assessments can be corrected before using them as part of the decision-making process (Lindley 1982, Lindley 1983, Morgan 2014).

## GOALS AND CONTRIBUTIONS

The goals and contributions of this thesis are: 1) to study and to provide novel perspectives on temporal and density-dependent variability in the reproduction of marine fishes through their recruitment dynamics, 2) to develop new statistical models and prior distributions that are better suited for recruitment modelling, 3) to examine the validity of the common assumptions by applying the methods to empirical data on marine fishes, and 4) to provide numerical algorithms for parameter inference in the models.

Articles [I] and [II] provide methods for detecting sudden changes in fish recruitment dynamics and models that can better adapt to these changes. The adaptive models allow parameter estimates to change suddenly, which in turn results in model predictions that take the changes in the system into account, thus providing more up to date information about the stocks than traditional models. This is all done using formal Bayesian statistical framework instead of frequentist or ad-hoc tools that have been the state-of-the-art up to now.

In Article [I], recruit-per-spawner (RPS) ratios for four Atlantic cod stocks are examined using Bayesian change point detection methods. The RPS ratio is a commonly used measure for the reproductive capability of a fish stock. The analysis shows that in addition to year to year variability around the mean level of the RPS time series, these stocks have experienced sudden changes also in the mean level, and a formal statistical methodology for detecting these changes, estimating the current mean and variance of RPS, and for making short term predictions is provided.

Article [II] expands the approach of Article [I] by assuming that the number of recruits is a non-linear function of the spawning stock biomass. The changes are detected in the parameters of this so-called stock-recruitment model. This is achieved by sequential numerical approximations to the posterior distribution of the model parameters within the same sequential change point detection framework used in Article [I]. The methodology is tested on four marine fish species in the southern Gulf of St. Lawrence, for all of which the allowance of sudden shifts in the parameters provide better fit and more up to date predictions about the future recruitment. In both articles ([I] and [II]) the proposed methodology is also tested using extensive simulations.

Article [III] deals with low-abundance recruitment dynamics. Traditionally it has been assumed that as the stock size decreases the per capita reproduction gets higher. This so called compensatory behaviour makes it possible to exploit the stocks heavily since they are bound to recover swiftly when the exploitation is stopped, or the fishing pressure is reduced. The traditional assumption of compensatory dynamics has been widely accepted in marine fish populations. In Article [III], the methodological limitations of some of the previous research is pointed out, and a formal probabilistic method to analyse the prevalence of compensatory dynamics is presented. Contradictory findings are reported for Atlantic herring (*Clupea harengus*) showing that depensatory (as opposed to compensatory) dynamics are more



common than previously thought. Also, formal method for acknowledging and handling the uncertainty related to the low-abundance dynamics using Bayesian statistical methods is presented.

Article [IV] focuses on modelling the subjective biases that experts may have in their assessments of key parameters relating to fish stock population dynamics. The experts' biases are modelled in non-hierarchical and hierarchical Bayesian setting, and three different models utilizing Gaussian processes for the experts' biases are developed. The novel fully Bayesian method for combining experts' assessment and simultaneously correct for their biases using supra-Bayesian approach (French 1980, Lindley and Singpurwalla 1986) is validated in simulations and applied to a real data set concerning the stock depletion parameter of 20 marine fish stocks.

## 2 DATA SOURCES

### 2.1 STOCK ASSESSMENT ESTIMATES

Direct observations of fish stock size and structure are impossible to make. To study questions related to the relationship between the stock size and the expected number of offspring each year, estimates are often used. It is customary to use stock assessment (SA) outputs in retrospective analysis (e.g. meta analyses on recruitment, low-abundance dynamics, etc.).

The use of stock assessment model outputs as data in post hoc analysis has been criticized since it is not observational data (Brooks and Deroba, 2015). However, this “data” often represents the best available knowledge about quantities that are otherwise impossible to observe directly and without error, and which are crucial to scientific research on plethora of topics in marine biology, ecology and population dynamics. Thus, the usefulness of such data in academic research cannot be disputed.

#### RAM LEGACY DATABASE

RAM Legacy Stock Assessment Database (RAMLDB; <http://ramlegacy.org>; Ricard et al. 2013) is a collection of stock assessment estimates for commercially exploited marine fishes and invertebrates from around the world. It is successor to the Myers’ Stock Recruitment Database which was created by Dr. Ransom A. Myers, Nick Barrowman and Jessica Bridson in the mid-1990s that has not been updated and maintained since 2004. RAMLDB offers a wide range of data to be used in research under a fair use policy. The data includes, but is not limited to, time series of estimates of total fish stock biomass, spawning stock biomass, number of recruits, catches and landings, and key stock assessment model parameters such as fishing mortality. The most recent version available at the website (v. 3.0) is assembled from stock assessments conducted by 33 national and international management agencies covering a total of 513 stocks. Since the first publication using RAMLDB in 2009, estimates from the database have been used in dozens of studies (e.g. Worm et al. 2009, Hutchings et al. 2010, Jensen et al. 2012, just to name a few).

This thesis utilizes stock assessment data obtained from RAMLDB in Article [I]. The data used in the analysis consists of estimates of the number of recruits and the spawning stock biomasses for four Atlantic cod (Figure 1) stocks, namely, northern cod, southern Gulf of St. Lawrence cod, Northeast Arctic cod, and North Sea cod. This data was used to detect shifts between different productivity regimes in these stocks.



**Figure 1.** The collapse of the Atlantic northwest cod fishery made cod the iconic study species for fisheries collapse and recovery. The cod in the picture were caught near Ramsøy in Norway (© Arnstein Rønning / Wikimedia Commons / CC-BY-SA-3.0 / GFDL)

## **ICES STOCK ASSESSMENT REPORTS**

The International Council for the Exploration of the Sea (ICES) is a global organization that develops science and advice to support the sustainable use of the oceans. ICES working groups produce annual stock assessment reports on dozens of marine fish stocks, mainly in Europe. They produce advice to policy makers and short and long-term forecasts about the development of the stocks. ICES working group reports are published on the ICES website ([ices.dk](http://ices.dk)). Estimates of stock size, number of recruits, and several other interesting quantities can be extracted from these documents to be used in subsequent analysis.

The data on spawning stock biomass and number of recruits used in Article [III], have been extracted from ICES working group reports (ICES 2015a, ICES 2015b, ICES 2015c). The data covers nine stocks of Atlantic herring, namely, Celtic Sea and South of Ireland, Gulf of Riga, Western Baltic spring spawners, Eastern Baltic, Bothnian Sea, West of Scotland and West of Ireland, Icelandic summer-spawners, Irish sea, and North Sea autumn spawners.

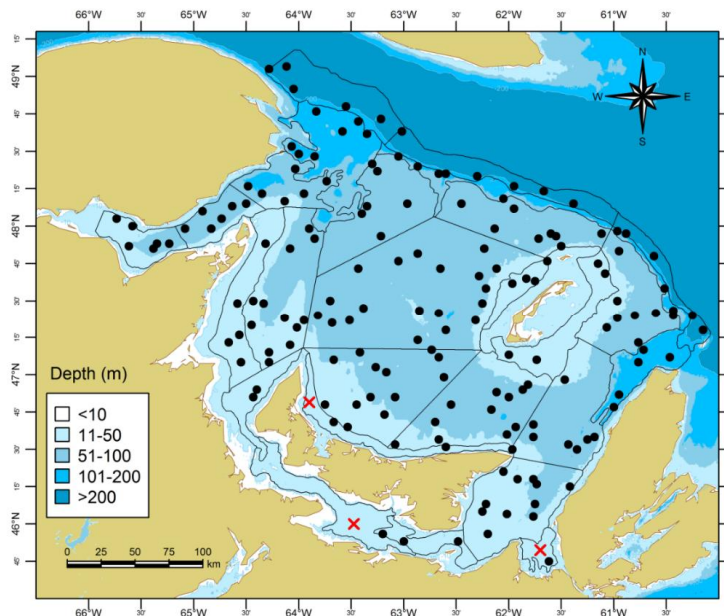
## **2.2 SURVEY DATA**

Another source of data on the status of marine fish populations is different surveys conducted by research vessels. These surveys sample a subarea of the whole area chosen by some criteria. The data obtained is then usually considered as a representative sample of the whole population.

Bottom trawl surveys are conducted by research vessels using a fishing net which is towed along the sea floor. Fish are then caught, and the catch is

measured to obtain an estimate of the length or weight composition of the population. A subset of the catch is further analysed to obtain data on age at length or age at weight, and maturity. These data can then be used as inputs to stock assessment models.

Bottom trawl survey data from Fisheries and Oceans Canada (DFO) conducted in the southern Gulf of St. Lawrence in Canada (Figure 2) since 1971 was used in the analysis of Article [II]. The data provided estimates of the average mass, the proportion of mature individuals, and the mean number of individuals in each age class. Estimates of the number of recruits and the spawning stock biomass were derived from this data. The species selected for this study were Atlantic cod, thorny skate (*Amblyraja radiata*), American plaice (*Hippoglossoides platessoides*), and white hake (*Urophycis tenuis*). The data was used in stock-recruitment modelling to examine if the relationship between the spawning stock size and the number of recruits remained constant for each species during the time frame.



**Figure 2.** Map of the southern Gulf of St. Lawrence in Canada. The Gulf of St. Lawrence is a unique marine ecosystem characterized by partial isolation from the North Atlantic, freshwater runoff from the land, a deep trough along its length, seasonal ice, the presence of a cold intermediate layer, shallow depths, and high biological productivity. Black circles show the locations of the fishing stations used in the 1989 survey, and red crosses indicate strata added in 1984 and omitted from the analyses to maintain consistent survey area. Figure is adopted from the supplementary material of Article [II]. Figure was produced by Douglas Swain.

## 2.3 EXPERT KNOWLEDGE

The real data application in Article [IV] uses data from a previous article by a co-author of Article [IV] (Chrysafi et al. 2017). Six experts with different levels of experience in stock assessment were divided into three groups of two based on their expertise level. The experts were given some background information relating to the fish stocks, and they were asked to formulate their opinion on the stock depletion status of the stocks as Beta-distributions using a web application developed for this purpose. The “true” parameter values were extracted from stock assessments from the U.S. Pacific Fishery Management Council (PFMC) and Alaska Fisheries Science Center (AFSC).

## 2.4 SIMULATED DATA

In addition to the previously described empirical data, all the articles in this thesis use simulated data to test the performance and validity of the methods, or to further analyse the properties of the used models. The number of recruits and the spawning stock biomass used for method validation in Article [I] were generated using an individual and process-based population dynamics model for cod (Kuparinen et al. 2012a, Kuparinen and Hutchings 2012, Kuparinen et al. 2014). In Article [II], model validation was conducted using simulated data on S and R. The S values were generated randomly, and the corresponding R value calculated using stochastic S-R relationships. Random shifts in model parameters were induced to simulate regime shifts in S-R dynamics. In Article [III], empirical data were used to generate artificial test cases by removing certain data points to study the effects of low-abundance observations on the uncertainty about the depensation parameter and model predictions. The models developed in Article [IV] were analysed in extensive simulation setting. A sigmoidal form for the expert’s bias was assumed, and the maximum level of bias, the level of noise, and the number of data points used for the model calibration were varied to test the models’ performance in different settings. The different types of data used in the articles of this thesis are shown in Table 1.

**Table 1** *The data sources used for the analysis and validation of the methods used in this thesis*

Article No.	Stock assessment estimates	Survey data	Expert assessments	Simulated data
I	X			X
II		X		X
III	X			X
IV	X		X	X

## 3 MODELS

### 3.1 STOCK-RECRUITMENT MODELS

In this work, two standard S-R models, namely, the Beverton-Holt (Beverton and Holt 1957) and the Ricker (Ricker 1954) models and their extensions are considered. Both standard models are compensatory models, i.e., as the stock size declines the number of recruits per unit of spawning stock increases. The gradient of the curves at the origin represents the maximum reproductive rate of the fish stock. The maximum reproductive rate is deemed as the most fundamental of all population parameters (Myers 1996), and it is widely accepted as the appropriate measure of the renewal potential of a fish stock. It also determines the highest level of fishing mortality that can be sustained in a deterministic equilibrium (Myers 2002).

#### BEVERTON-HOLT MODEL

The Beverton-Holt model can be derived from the so-called first principles, and it results from the assumption of contest competition, where some individuals obtain all they need, and others less than they need (Brännström and Sumpter 2005). The first principles derivation gives the model biological grounding. One widely used formulation of the Beverton-Holt S-R model is:

$$(1) \quad R = \frac{\alpha S}{1 + \beta S},$$

where  $\alpha$  is the maximum reproductive rate, and  $\beta$  controls the density dependence. The asymptotic maximum of this curve is  $R_\infty = \alpha/\beta$ , and thus  $\beta$  can be interpreted such that one half of the maximum number of recruits,  $\frac{1}{2}R_\infty$  is produced when the stock size  $S_{50} = \frac{1}{\beta}$ . The Beverton-Holt model may also be parameterized using  $\alpha$  and  $R_\infty$ , or  $R_\infty$  and  $S_{50}$  as

$$(2) \quad R = \frac{S}{\frac{1}{\alpha} + \frac{S}{R_\infty}}, \quad R = \frac{R_\infty}{1 + \frac{S_{50}}{S}},$$

respectively. The first parameterization of the Beverton-Holt model was used in Article [II] and the third in Article [III].

### SIGMOIDAL BEVERTON-HOLT MODEL

The Sigmoidal Beverton-Holt (SBH; Myers et al. 1995) model is obtained as an ad-hoc extension of the Beverton-Holt model by introducing a third parameter,  $c$ , which is called the depensation parameter. The model in Article [III] was parameterize using  $R_\infty$ ,  $S_{50}$  and  $c$  as

$$(3) \quad R = \frac{R_\infty}{1 + \left(\frac{S_{50}}{S}\right)^c}.$$

This model provides more flexibility, especially at low stock sizes. When  $c = 1$ , the model reduces to the Beverton-Holt model,  $c < 1$  yields a model with greater amount of compensation than the Beverton-Holt model, and  $c > 1$  produces depensatory recruitment model.

### RICKER MODEL

The Ricker model can be derived from scramble competition, which assumes that the individuals in the fish population are distributed uniformly at random, and their reproductive success is rapidly reduced by competition with neighbours (Royama 1992, Brännström and Sumpter 2005). One parameterization of the model is

$$(4) \quad R = \alpha S e^{-\beta S},$$

where  $\alpha$  is the maximum reproductive rate, and  $\beta$  describes the density-dependence. The Ricker model is dome-shaped, and the maximum number of recruits, often called the carrying capacity,  $K = \frac{\alpha}{e\beta}$ , is obtained when the stock size is  $S_K = \frac{1}{\beta}$ . The model can also be parameterized using  $\alpha$  and  $K$ , or  $K$  and  $S_K$  as

$$(5) \quad R = \alpha S e^{-\frac{\alpha}{eK}S}, \quad R = K \frac{S}{S_K} e^{1 - \frac{S}{S_K}},$$

respectively. The first parameterization was used in Article [II] and the third in Article [III].

### SAILA-LORDA MODEL

The Saila-Lorda (S-L; Saila et al. 1988, Iles 1994) model is an ad-hoc extension of the Ricker model. By introducing a depensation parameter,  $c$ , a more flexible model is obtained. We parameterized the S-L model in Article [III] using  $K$ ,  $S_K$  and  $c$  as

$$(6) \quad R = K \left( \frac{S}{S_K} \right)^c e^{c \left( 1 - \frac{S}{S_K} \right)}.$$

When  $c = 1$ , the model reduces to the Ricker model,  $c < 1$  yields a model with more compensation than the Ricker model, and  $c > 1$  produces a model with depensatory recruitment dynamics.

### VISUALIZING THE DIFFERENCES

The Sigmoidal Beverton-Holt and the Sella-Lorda models are shown in Figure 3 for three cases:  $c < 1$ ,  $c = 1$ , and  $c > 1$ . The difference between the standard models and their extended versions is seen in the curves describing the expected number of recruits. However, regarding the uncertainty of the low-abundance dynamics, even more important difference between these models is seen in the posterior predictive distribution of the number of recruits as a function of the spawning stock biomass. Figure 5 presents the difference in the predictions between the Beverton-Holt and Sigmoidal Beverton-Holt models fitted to the Western Baltic spring spawning herring stock assessment estimates.

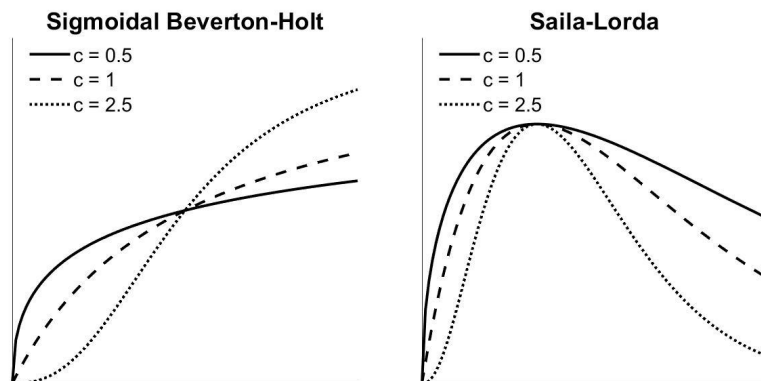


Figure 3 Demonstration of the effect of the ‘depensation parameter’ in the Sigmoidal Beverton-Holt and Sella-Lorda stock-recruitment models. When  $c = 1$ , the models reduce to the Beverton-Holt and Ricker models, respectively.

### 3.2 CHANGE POINT MODELS

Change points are abrupt changes in the parameters of the data generating model. Basically, the aim of change point detection is to divide a sequence of observations into non-overlapping product partitions. When modelling a system, each partition can have a different set of parameters, and thus the system can behave differently.



In this work, the Bayesian online change point detection (BOCPD; Adams and MacKay 2007) approach is used. In BOCPD, the change points are modelled using an auxiliary variable called *run length*. The run length is a discrete variable that describes the time since the last change point. The data points are considered sequentially, and when transitioning from one time step to the next, the run length either grows by one or goes to zero indicating that a change point has occurred. BOCPD offers a modular framework, which conveniently separates the implementation of the change point algorithm and the implementation of the data generating model. The concept of the run length and the BOCPD algorithm require more explanation to be fully understood. However, since the explanation is lengthy, and it has been already done in the two articles of this thesis, the explanation is omitted here, and the interested reader is encouraged to see Articles [I] and [II] for more details.

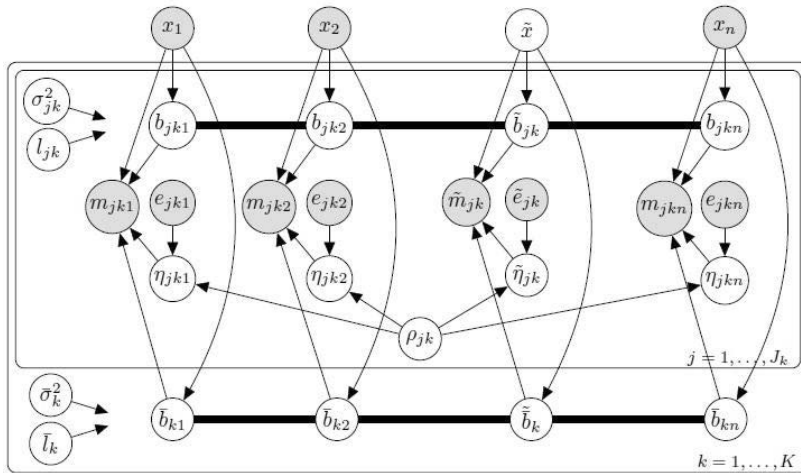
### **3.3 EXPERT BIAS MODELING USING GAUSSIAN PROCESSES**

In environmental management, expert assessment is an essential source of information especially when observational data is scarce. The use of experts' point estimates and their uncertainty about the estimates is widely regarded as an important part of decision making (O'Hagan et al. 2006). Traditionally, multiple experts are asked for their opinions on the subject matter, and the opinions are pooled together by simply taking the average of the experts' estimates or by using some other straight-forward method of combining the expert assessments. These approaches assume that the experts are unbiased in their judgements. However, the expert assessments can be biased, and the experts can severely underestimate their own uncertainty about their assessments. To be more useful for decision making, the expert assessments should be corrected for the biases. When the biases are systematic, it should be possible to use statistical models to infer and correct for the bias when calibration data is available.

In Article [IV], a fully Bayesian approach for combining expert assessments using supra-Bayesian approach is presented (French 1980, Lindley and Singpurwalla 1986). Supra-Bayesian approach allows not only for rigorous combination of the expert assessments but also for the inference and correction of the biases. The expert assessments are assumed to contain subjective biases, and the expert's mean estimate,  $m$ , of an unknown parameter,  $x$ , is assumed to depend on the "true" parameter value but it is affected by some unknown bias function,  $b(x)$ . The bias is also assumed to depend on the true parameter value, and it is modelled using Gaussian processes (Rasmussen and Williams 2006). Three different models for the bias is used: 1) the bias is additive, 2) the bias is additive in the logit-space, and 3) assuming a uniform prior for the mean estimate of the expert. Also, the effect of considering experts' uncertainty estimates of their assessment is

tested, and their overconfidence is corrected for. In addition to considering the experts mutually independent, a hierarchical model is tested where the experts are divided into groups based on their expertise on the subject matter. It is assumed that the experts within the same group share some characteristics in their biases. Figure 4 shows the hierarchical model used in Article [IV].

In the motivating real-life example of Article [IV], the unknown parameter is the ratio of the current and the virgin biomass of an exploited fish stock. Expert assessments for 20 fish stocks are used, and the methods' performance is evaluated using cross-validation.



**Figure 4** Graphical representation of the expert bias correction model. Grey circles denote the observed nodes, i.e., the calibration data  $(x_i, m_{jki}, e_{jki}), i = 1 \dots n, j = 1 \dots J_k, k = 1 \dots K$  and the experts' mean and uncertainty estimates for the unknown parameter,  $\hat{x}$ , in a new system  $(\tilde{m}_{jk}, \tilde{e}_{jk}), j = 1 \dots J_k, k = 1 \dots K$ . The thick lines denote the Gaussian fields.

## 4 MODEL FITTING AND PARAMETER ESTIMATION

### 4.1 BAYESIAN INFERENCE

Bayesian inference is a powerful tool for fitting statistical models to data, and to predict future behaviour of the system. Bayesian approach to modelling and handling uncertainties is superior to all the other approaches since it is the only approach that uses a probability measure for parameter and structural uncertainties. The inference consists of two steps: 1) the formulation of the current knowledge or beliefs about the phenomenon in the form of a prior distribution, and 2) the updating of the knowledge when new evidence or information becomes available.

The updating of beliefs with new evidence or information (also called learning) is carried out using the law of conditional probability, a fundamental concept of the theory of probability. The cornerstone of Bayesian learning is the Bayes' theorem, which can be written mathematically as

$$(7) \quad P(X|I) = \frac{P(I|X)P(X)}{P(I)},$$

where  $X$  refers to some event or hypothesis we want to learn about, and  $P(X) \in [0,1]$  represents our knowledge about or the degree of belief in  $X$  expressed in terms of probabilities before considering the new information or evidence  $I$ , which is assumed to carry information related to  $X$ .

In the context of Bayesian inference, the knowledge before receiving new evidence,  $P(X)$ , is called the prior probability of  $X$ . The conditional probability of receiving the new piece of evidence given that the event  $X$  happened, or the hypothesis  $X$  is true,  $P(I|X)$ , is used to construct the likelihood function  $L(X|I) \propto P(I|X)$  after receiving the evidence  $I$ . The likelihood function describes how likely  $X$  is given the new evidence. The term in the denominator,  $P(I)$  is the marginal prior of  $I$ , which can be used to construct the marginal likelihood of the model. The marginal prior is usually ignored since it only acts as a normalizing factor in the equation and does not affect, for example, the relative probabilities of competing hypothesis. Also, the computation of the marginal likelihood is often extremely difficult, and thus ways to circumvent the computation in inference problems have been developed. The resulting updated degree of belief, which is a combination of the prior knowledge and the new evidence,  $P(X|I)$ , is called the posterior probability of  $X$ .

The beauty of Bayesian inference lies in the fact that any information about  $X$  that can be expressed in the form of a likelihood can be used to update the knowledge using the same Bayes' theorem.

## SEQUENTIAL UPDATE

Often, information about phenomena becomes available at different times. For example, surveys of natural resources may be carried out once every year. Bayesian inference offers an easy way to update our beliefs whenever new pieces of information are obtained. Philosophically, the old posterior, which is the combination of the original prior and the likelihood of the previous piece of information, becomes the new prior which is then updated using the newly obtained information. This way of updating the beliefs is called *sequential update* or *sequential estimation*.

Let us denote the new piece of information by  $I_{new}$ . Using the Bayes' rule, the posterior obtained using both pieces of information may be written as

$$(8) \quad P(X|I, I_{new}) = \frac{P(I, I_{new}|X)P(X)}{P(I, I_{new})}.$$

If we now assume that the new information is independent of the old information  $I$ , the *joint probability* can be written as a product of the individual probabilities, i.e.,  $P(I, I_{new}|X) = P(I|X)P(I_{new}|X)$ . Also, by the laws of conditional probability, the *joint marginal prior* can be written as  $P(I, I_{new}) = P(I_{new}|I)P(I)$ . After substituting these equations and rearranging the terms, the posterior is

$$(9) \quad P(X|I, I_{new}) = \frac{P(I|X)P(X)}{P(I)} \frac{P(I_{new}|X)}{P(I_{new}|I)}.$$

Now, we notice a familiar expression on the left of the right-hand side, and can substitute equation (7) to get

$$(10) \quad P(X|I, I_{new}) = \frac{P(X|I)P(I_{new}|X)}{P(I_{new}|I)}.$$

The above equation looks exactly like equation (7) if we interpret  $P(X|I)$  as the new prior.

There are several benefits in this kind of sequential formulation of the Bayes' theorem. Firstly, as all the information interpreted from the data is already incorporated in the posterior distribution, the data can be discarded, since it is not used in future updates. This can be beneficial in cases where the datasets are huge, and their storage is expensive. Secondly, a single sequential update step is computationally much less expensive than carrying out the full update using all the data. Also, analysing the sequence of distributions may provide more insight to the studied phenomenon compared to the final posterior distribution.

Sequential estimation is used in Articles [I] and [II] of this thesis, since the BOCPD algorithm is sequential.

## SMOOTHING

In the sequential update, the posterior distribution is inferred after the arrival of each observation, or at some fixed time steps. This produces posterior distributions that tell what is the state of knowledge at time  $t$  when all the information obtained up to time  $t$  have been considered. In some applications this *forward filtering* can produce noisy sequences of estimates, and the estimates can be influenced by outliers in the data. This behaviour was encountered in Articles [I] and [II], where it was noticed that the models could produce a high posterior probability for a regime shift based on only one anomalous observation. It is of course desirable that the model can quickly warn when a sudden change might have happened, but when analysing the historical development of the system, an approach that would take all the data into account to find the segmentation of the data is needed. This prompted the use of *smoothing* (Särkkä 2013), which produces conditional probability distributions for each time step given all the data, past, current, and future.

## PRIOR DISTRIBUTIONS

The likelihood is a familiar concept also in frequentist statistics as the description of the relationship between the model parameters and the data. The prior, however, is a purely Bayesian concept, and it acts as a convenient way of expressing the background information about the phenomenon under study. The use of informative prior distributions also allows us to make inference in problems where frequentist methods might not be able to produce any estimates, for example by giving more weight to certain areas of the parameter space, when the solution based on likelihood only would be ambiguous.

As the prior clearly affects the posterior, Bayesian inference produces, by definition, subjective probabilities. As two persons might have different background information, and thus different priors, these two persons would end up with differing posteriors. This is reasonable, since it can be argued that a truly objective point of view does not exist. Even frequentist statistics is subjective since it is based on a subjective point of view on how the empirical  $P(I|X)$  would look like if the data collection could be repeated indefinitely. Thus, the posterior distribution is subjective also because of the modeller's choice of the likelihood function.

However, sometimes we want to play ignorant and minimize the effect of the prior on the inference by using uninformative priors or so-called reference priors (Article [II]). Also, by using uninformative priors, we can ensure that we do not favour one outcome over the others when testing competing hypothesis (Article [III]).

Formulating our background knowledge, or the lack there of, into a probability distribution is not always a straight-forward task. When asking someone with little or no training in probabilities to formulate their knowledge as a probability distribution, the result might not be an accurate

representation of their knowledge. It is also possible that the subjective assessment of the state of the nature is affected by psychological biases, which if possible, would be beneficial to correct for before using the knowledge as a prior distribution in inference (Article [IV]).

Sometimes, when there is no a priori knowledge of the phenomenon under study we must carefully analyse and understand the models we use to be able to assign priors that truthfully reflect our ignorance about the quantities of interest. We might even face a situation where suitable off-the-self prior distributions are not available, and end up developing our custom priors to make sure we give equal prior probabilities to competing hypothesis (Article [III]).

## **PREDICTION**

In Bayesian statistics, predicting the next piece of information is carried out using the posterior predictive distribution  $P(I_{new}|I)$ . The posterior predictive distribution is defined as the integral of the conditional distribution of the new piece of evidence given  $X$  times the posterior distribution of  $X$  over the parameter space

$$(11) \quad P(I_{new}|I) = \int_X P(I_{new}|X)P(X|I)dX$$

The posterior predictive distribution was used to demonstrate the model fits in Articles [I]-[III] of this thesis.

## **4.2 SOLVING THE POSTERIOR DISTRIBUTIONS**

Although the Bayes' formula is quite simple and easy to understand, it does not yet provide the full description of the model or tell how to estimate the parameters of interest or how to calculate predictions. The modeler must provide the probability density functions, and plug them into the Bayes' update formula. Unfortunately, only in a small subset of problems, it is possible to solve the posterior distribution of the parameters analytically, and thus computationally intensive numerical methods are often used.

### **ANALYTICAL SOLUTIONS**

For certain problems it is possible to solve the posterior distribution analytically. These problems usually consist of a model where the data is a linear function of the parameters. Moreover, the prior distribution must be chosen from a certain family of distributions that consists of the so-called *conjugate priors* for the likelihood function.

In Article [I], a normal-gamma prior is used as the joint prior distribution of the mean and precision parameter of the data-generating model together with a Gaussian likelihood function. This ensures that the posterior distribution of the parameters is also a normal-gamma distribution. The prior and posterior distributions are fully described by their *hyperparameters*, and the hyperparameters of the resulting posterior distribution can be calculated from the hyperparameters of the prior distribution and the data using simple arithmetic recursions. This, enables us to sequentially and analytically solve the joint posterior distribution of the run length and the unknown mean and precision parameters of the data generating model.

## NUMERICAL METHODS

For most fisheries models, analytical solutions are not available. However, if a posterior sample of the parameters is available, it can be used to approximate probabilities  $P(X \in A)$ , for example, central probability intervals (CPI), to generate a histogram, or to approximate integrals of functions of the parameters (expectations). While the former two are easy to understand, the approximation of the integrals requires a little more explanation. The sample can be used to approximate the target distribution with an empirical point-mass function

$$(12) \quad P_N(X) = \frac{1}{N} \sum_{i=1}^N \delta(X - X^i),$$

where  $X$  is the random variable whose distribution we are interested in,  $X^i, i = 1, \dots, N$  is the sample, and  $\delta(\cdot)$  is the Dirac delta function. Let  $g(X)$  be some function of  $X$ . The expected value of  $g(X)$  is denoted by  $E(g(X))$ , and it is defined as the integral over the domain of  $X$  of  $g(X)p(X)$ , where  $p(X)$  is the probability distribution of  $X$ . Approximating the probability distribution with the empirical point-mass function the expectation can be written as

$$(13) \quad E(g(X)) \approx \int_X g(X)p_N(X)dX = \frac{1}{N} \sum_{i=1}^N g(X^i).$$

It is often difficult to directly sample from the posterior distribution. However, methods for producing independent samples from arbitrary posterior distributions have been developed. Next, some numerical methods for sample based posterior estimation are described, namely, the Markov chain Monte Carlo and sequential Monte Carlo methods.

### **Markov Chain Monte Carlo**

Markov Chain Monte Carlo (MCMC) methods are algorithms that can be used to produce samples from probability distributions. This is achieved by

constructing a Markov chain whose equilibrium distribution is the probability distribution one wishes to draw samples from. MCMC methods are used for Bayesian inference and numerical integration.

The Metropolis algorithm (Metropolis et al. 1953) is the first MCMC method developed. It works by generating a sequence of samples (chain) in the parameter space using random walk. The chain is initialized at some point and a candidate for the next point is drawn from a proposal distribution. The proposal distribution is some simple, easy to sample from distribution, usually Gaussian centred at the previous point in the chain.

Next, the *acceptance ratio*  $r = P(X'|I)/P(X_t|I)$  is calculated, where  $X'$  is the candidate point and  $X_t$  is the last point in the chain, and  $P(X|I)$  is now the posterior distribution of the parameters of the model we are interested in. The candidate point is then rejected with probability  $1 - r$  in which case a new candidate is drawn or otherwise accepted, and the algorithm proceeds to producing the next sample in the same fashion.

Usually when  $P(X|I)$  is the posterior distribution one wishes to draw samples from, it is not known (which was the reason why the samples were needed in the first place). However, the ingenuity of the Metropolis algorithm, and its suitability for Bayesian inference lies in its property that the marginal likelihood does not need to be known, and it suffices that the posterior distribution is known up to a proportionality constant, which it almost always is, because

$$(14) \quad r = \frac{P(X'|I)}{P(X_t|I)} = \frac{\frac{P(I|X')P(X')}{P(I)}}{\frac{P(I|X_t)P(X_t)}{P(I)}} = \frac{P(I|X')P(X')}{P(I|X_t)P(X_t)}.$$

In the Metropolis algorithm, the proposal distribution must be symmetric, but this constraint was later relaxed in the Metropolis-Hastings algorithm (Hastings 1970), which is a generalization of the Metropolis algorithm. The Metropolis-Hastings algorithm can be very efficient in low-dimensional parameter spaces. However, when the number of parameters grows another approach is needed.

The most commonly used algorithm for fitting Bayesian fisheries models is called the Gibbs sampler. The Gibbs sampler is a special case of a Metropolis-Hastings algorithm, where the parameter vector is divided into  $d$  components, and each iteration of the sampler cycles through the  $d$  components of the parameter vector and draws the corresponding elements of the parameter vector from their marginal distribution conditional on the other components' values. The Gibbs sampler is easy to implement, but it is known to suffer from poor mixing (i.e., subsequent samples are correlated and thus not mutually independent), and problems with convergence (i.e., Markov chain not reaching its equilibrium state). These problems are present in models where considerable posterior correlation occur between model parameters, and especially for high-dimensional problems.



One way to reduce the correlation and improve the convergence is to utilize the gradient of the posterior density function (more accurately log-posterior). This is the basic idea behind Hamiltonian Monte Carlo (HMC) algorithms (also called Hybrid Monte Carlo). HMC avoids random walk behaviour by using Hamiltonian dynamics to more efficiently explore the interesting areas of the parameter space. Implementation of HMC algorithms is, however, much more complicated than MCMC algorithms that are purely based on random walk. HMC requires a careful tuning of several parameters and its performance is highly dependent on these parameters that are model dependent (Hoffman and Gelman 2014). To be more usable for people with less skill and experience in algorithm tuning, the No-U-Turn Sampler (NUTS; Hoffman and Gelman 2014) was developed. NUTS automatically tunes the parameters and is thus easier to use. HMC was used in fitting the time-invariant models in Article [II], and all the models in Articles [III] and [IV].

### **Sequential Monte Carlo**

As opposed to the MCMC methods that use all the data at once, it is also possible to formulate the posterior inference problem sequentially as was shown in Section 4.1.1. Sequential Monte Carlo methods (SMC; also known as *particle filters*) is a class of algorithms that can be used to produce posterior samples sequentially. As with the MCMC methods, several SMC variants exist. SMC methods are usually applied to state space models, where the model consists of a dynamic state vector (and possibly static parameters). Here, instead of the random sample, a weighted sample is considered, meaning that each realization in the sample has a corresponding weight attached to it. The weights are non-negative, less than one, and sum up to one.

The basic idea behind SMC algorithms is simple. First, draw a sample from the prior and assign equal weights to each individual sample point. When a new data point is obtained, update the weights based on the likelihood values of the sample points. If there are dynamic parameters, propagate the sample to the next time step using the state model. If too many of the samples have weight close to zero, resample.

The SMC variant used in Article II uses the idea of artificial evolution of parameters to avoid particle degeneracy (Liu and West 2001). Since the problem was to infer static parameters, the posterior sample would degenerate quickly. Thus, the sample points were resampled regularly, which guaranteed that the method worked properly.

## **4.3 SOFTWARE**

The algorithms used for fitting the change point models in Articles [I] and [II] were implemented in MATLAB, which is a numerical computing software and programming language developed by MathWorks. The models in Articles [III]

and [IV] (and the time-invariant models in Article [II]) were fitted using Stan (Stan Development Team 2016a) via MatlabStan (Stan Development Team 2016b), a Stan interface for MATLAB. Stan is a free open-source software and programming language for Bayesian statistical modelling and inference, which implements the No-U-Turn variant of the HMC sampler, and provides an easy way to implement statistical models and carry out the inference. All analysis was carried out and figures were produced with MATLAB.

## 5 RESULTS

### 5.1 DETECTING REGIME SHIFTS IN FISH POPULATION DYNAMICS

The change point detection algorithm applied to the time series of recruit-per-spawner ratios for four Atlantic cod stocks in Article [I] found several productivity regimes for each stock. However, for the North Sea cod, the parameterization of the algorithm failed, which resulted in too many change points close to each other. The analysis indicates that the stocks have entered low productivity regimes in 1990s and 2000s.

By comparing the mean of the posterior predictive density of the change point model with the sample mean in the simulations, it can be seen how the method is clearly superior to the sample mean estimator when there are abrupt shifts in the mean level of the recruit-per-spawner ratios (Figure 1. of Article [I]).

### 5.2 ACCOUNTING FOR PARAMETER CHANGES IN S-R MODELS

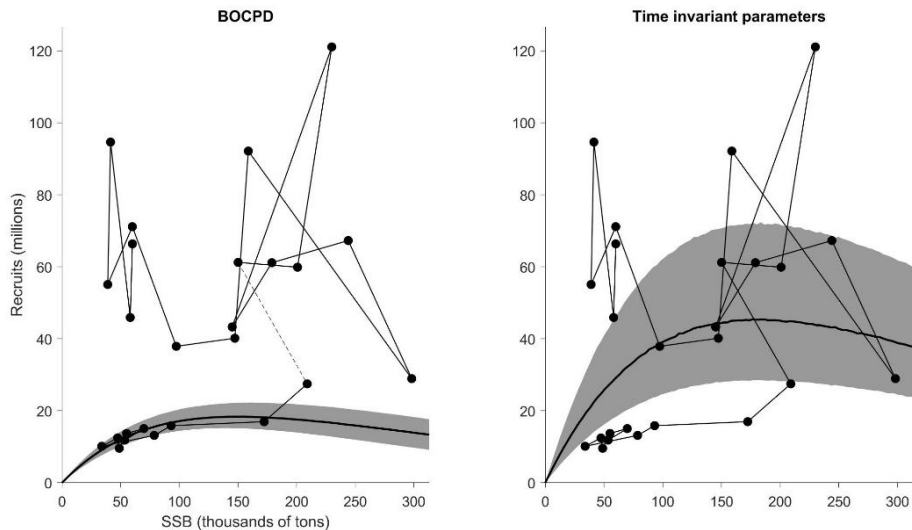
The stock-recruit modelling of four fish species in southern Gulf of St. Lawrence using change point models in Article [II] showed that none of the stocks' recruitment dynamics can be accurately described by a model assuming time-invariant parameters. Several shifts in the parameters of the models were found for each species, and the number of shifts and the timings of the shifts were almost identical for both the Ricker and the Beverton-Holt S-R models. The results were also quite robust to the choice of the prior distributions of the parameters and the change point prior probability.

The shifts caused huge changes in the posterior marginal distributions of the parameters (Figure 4 of Article [II]). For both S-R models, the parameter most affected by the shifts was the maximum recruit production per unit of spawning stock biomass ( $\alpha$ ) while the parameter describing the density dependent effects,  $\beta$ , did not change as much. Thus, the changes in the maximum number of recruits,  $K$  or  $R_{\infty}$ , derived from the model parameters mimicked the changes in  $\alpha$  for both S-R models. The relative changes in the median of  $\alpha$  ranged roughly between -75% and 750%. The changes in the parameters were also clearly visible in the model fits as represented by the posterior predictive distributions of the recruits as a function of the spawning stock biomass (Figure 6. of Article [II]).

In contrast, models assuming time-invariant parameters fitted to the same data did not react to the shifts nearly as fast as the change point model, and they also failed to produce accurate uncertainty estimates but instead

consistently underestimated the uncertainty related to the parameters. The parameter distributions of the time-invariant model did slowly start to move towards the parameter distributions produced by the change-point model, but it could take more than a decade to reach the same level, if at all. This tendency of the time-invariant model parameter estimates to approach the change point model parameter estimates further supports the findings that the four stocks studied have indeed experienced dramatic shifts in their recruitment dynamics.

The difference in the behaviour of the time-invariant model and the change point model is illustrated in Figure 5.



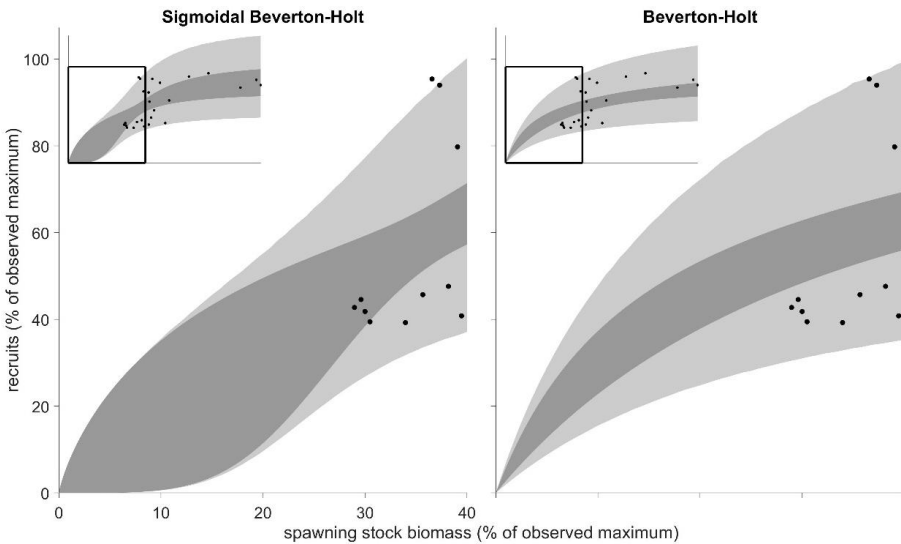
**Figure 5** Comparison of the model fits of the Ricker S-R model with time-invariant parameters and using BOCPD. The grey area denotes the 50% CPI of the posterior predictive distribution of the number of recruits as a function of spawning stock biomass. The data points used for fitting the models are shown as black dots. The shift to lower recruitment regime found by our method is denoted with a dashed line in the left panel. None of the points after the shift are inside the 50% CPI of the time-invariant model whereas the BOCPD model captures them well. The stock in question is the Atlantic cod in the southern Gulf of St. Lawrence.

### 5.3 EXAMINING LOW-ABUNDANCE DYNAMICS

The stock-recruit modelling in Article [III] showed that within the same species different populations may experience either compensatory or depensatory population dynamics. The statistical support for depensatory and compensatory dynamics in the nine Atlantic herring stocks studied provided by the posterior marginal probability distributions of the depensation parameter was quite evenly distributed. Four stocks showed strong evidence for depensatory dynamics whereas strong evidence for compensatory

dynamics was found for four populations while the evidence for one population was ambiguous although slightly more in favour of compensatory dynamics.

The systematic removal of the low-abundance observations shed light on the importance of low-abundance observations for making inference on the nature of low-abundance dynamics. It was also found that the S-R models that allowed for depensation were able to more realistically describe the uncertainty related to the low-abundance dynamics in the absence of low-abundance observations. The uncertainty was seen in the widespread posterior marginal distributions of the depensation parameter, and this lack of knowledge about the depensation parameter was also present at low abundances in the posterior predictive distribution of R as a function of S. On the contrary, the traditional Ricker and Beverton-Holt models admit very little uncertainty about the low-abundance dynamics. This difference is illustrated in Figure 6 where the posterior predictive distributions for the number of recruits produced by the Sigmoidal Beverton-Holt and Beverton-Holt models fitted to Western Baltic spring spawning herring data are compared.



**Figure 6** Comparison of the low-abundance behaviour of SBH and BH models in absence of low-abundance observations. The dark grey and the lighter grey areas denote the 90% CPI of the expected value and the posterior predictive distribution of R as a function of S, respectively. The data used for fitting the models are shown as black dots. The stock in question is the Western Baltic spring spawning herring. The compensatory BH model admits very little uncertainty at low abundances (0-20% of observed maximum S) even though no observations at less than 25% of observed maximum S exist. Instead, BH model predicts steeply increasing low-abundance S-R relationship. On the contrary, the SBH model produces huge uncertainty at low abundances reflecting the lack of low-abundance observations. Moreover, the uncertainty is not only larger in the predictions but also at the expected value of the model. Note also that at higher abundances where observations exist there is only little difference between the predictions of the two models.

## 5.4 CORRECTING FOR EXPERTS' BIASES

The validation of the methods developed for combining the experts' beliefs using simulated data showed that regardless of the bias model used, the simulated bias function was inferred with good accuracy (Article [IV]). In the simulations, the number of data points used for the inference, the amount of noise in the data, and the maximum bias level were varied. As expected, the accuracy increased with less noisier data and with more data points, and decreased with bigger maximum bias. There was, however, some differences in the performance between the different bias models, and the additive bias model, which was the model that was used to generate the data, performed slightly better than the others.

The methods' ability to infer the unknown parameter value for a new system was also tested in simulations, and the same trends were found when varying the simulation parameters. However, less difference between the three bias models was present than in the bias inference.

When applying the methods to the real data set described in Section 2.3, the model assuming a uniform prior for the mean estimate of the expert performed best. When evaluating the methods' performance in terms of the average log predictive densities (LPD), the methods only slightly outperformed uniform random guess. However, the average was found to be affected greatly by few random outliers in the real data, and it was found that two of the six experts used were very bad and inconsistent in their statements. The use of hierarchical models did not improve the parameter inference.

## 6 DISCUSSION

This thesis consists of four original research articles that provide formal statistical tools for accounting for uncertainty caused by temporal and density-dependent variability in fish stocks as well as for accounting for experts' biases and problems with estimating their own uncertainty when combining expert knowledge for use in fisheries stock assessment. In addition to the methodology developed in this thesis, new insights to temporal variability (regime shifts) and low-abundance dynamics (Allee effects) in marine fish populations were provided by the application of the methods to empirical data sets.

All models used in this thesis utilize the Bayesian approach for uncertainty modelling and statistical inference. The models in Article [II] and [IV] have not been published anywhere before. The model in Article [I] has been used elsewhere but not in the context of fisheries. The developed prior distribution for the depensation parameter in the models of Article [III] is novel, and to the author's knowledge the SBH and S-L models used in the article have not been previously analysed to the same extent using Bayesian statistical framework. Article [III] also provides novel viewpoints to the discussion surrounding the prevalence of Allee effects in marine fish populations, and points out methodological flaws in previous studies on the topic.

Before the publication of Article [I], the short-term predictions for the studied stocks produced by their respective stock assessment reports did not use all historical data but instead used only a few recent years estimates (Swain et al. 2012, DFO 2013, ICES 2012a, ICES 2012b). The finding of Article [I] that all the stocks have entered a low productivity regime quite recently supports this approach. However, none of the stock assessment reports used a probabilistic change point model to infer when the current regime has started. The method proposed in Article [I] could be applied to making these predictions so that the uncertainties about the timings of the change points and the model parameters are formally considered, and the uncertainty in the predictions more realistically reflects the true uncertainty present. The proposed method also anticipates coming shifts by assuming small prior probability of a regime shifts each year which then contributes to the uncertainty expressed by the posterior predictive distributions (Article [I]).

It can be argued that the approach to productivity regime shifts detection using the stock assessment estimates of recruit-per-spawner ratios is too simplistic since the data generating model does not account for density dependent nor environmental effects on recruitment (Article [I]), and the stock assessment estimates are biased by the underlying stock assessment model used to produce the estimates (Brooks and Deroba 2015). However, the change point detection was shown to work correctly in simulations (Article [I]), and thus the method can be added to the toolbox of regime shifts detection

algorithms for fisheries related data as the Bayesian alternative to the frequentist STARS algorithm.

Articles [I] and [II] support the emerging view that fish stocks can experience rapid shifts from one state to another with very different dynamics (Holbrook et al. 1997, Beaugrand 2004). Thus, it is crucial to take the possibility of regime shifts into account when modelling fish populations (King et al. 2015). When incorporated into stock assessment the change point models may provide more accurate insight to the historical development of the stocks, and they provide more truthful consideration of the uncertainties when inferring the status of the population as well as in predicting the stocks development in the future (Articles [I] and [II]).

As the stock-recruitment relationship is often used to model the reproduction of fish populations (Hilborn and Walters 1992), which is also a proxy to the fish stocks recovery ability and resilience of fishing (Hilborn and Walters 1992), it is paramount for sustainable fish stock management to be able to detect and react to changes in this relationship (King et al. 2015). If these changes are not accounted for, the predictions about the productivity of the fish stock may be grossly over-estimated and the risk of over-exploiting the stock grows. The novel methodology developed in Article [II] could be used to model stock-recruitment relationships in a manner that allows for shifts in the parameters of the relationship and takes the uncertainties related to the current state of the productivity of the stock and the model parameters into account and properly propagates the uncertainties into predictions of the stock's recruitment dynamics in the future. The methodology should also be applied to other fish stocks than those studied in Article [II] to find out if they have experienced shifts in their recruitment dynamics.

The findings of Article [III] suggest that S-R models that allow for either depensation or compensation should be preferred over models that assume only compensatory dynamics. There are several reasons for this. Firstly, there is a priori no scientific basis to assume compensatory dynamics unless proven otherwise. Secondly, allowing for depensation in S-R models does not significantly increase the model complexity, since there is only one parameter more compared to the traditional models (Iles 1994, Myers et al. 1995). Moreover, if the population experiences strictly compensatory dynamics, the models used in Article [III] that allow for depensation will behave very similarly to those assuming compensation.

The findings of Article [III] were conflicting with previous studies (Keith and Hutchings 2012, Hilborn et al. 2014), and the reasons for this were also investigated. Issues related to the choice of prior distributions and model selection procedures in the previous studies (Hilborn et al 2014) were identified as possible reason. Also, the standardization of the data at the level of species as opposed to the level of population (Keith and Hutchings 2012) was found to affect the conclusions drawn from the analysis (Article [III]).

The results question the validity of at least some of the previous studies on the prevalence of Allee effects in marine fish populations, suggest that



depensatory dynamics might not be as rare as previously thought (Hutchings and Kuparinen 2014, Hilborn et al. 2014, Hutchings 2015), and propose to use models flexible enough that allow for both depensation and compensation, and permit more uncertainty about the low-abundance dynamics when low-abundance observations are lacking. Based on the study it seems that less is known about the Allee effects and their prevalence than was previously thought, and acknowledging and better accounting for the Allee effects is crucial for sustainable exploitation strategies of marine fish populations.

The expert bias correction method developed in Article [IV] provides a novel semi-parametric tool for combining experts' knowledge and incorporating calibration data into the model. Moreover, the model uses a formal supra-Bayesian approach (French 1980, Lindley and Singpurwalla 1996) for this end instead of heuristic or ad-hoc approaches.

The expert bias correction models used Beta-distribution as the conditional distribution of the experts' mean estimate given the model parameters and the calibration data. Based on the results of the real data tests, the suitability of the Beta-distribution became questionable. With increasing uncertainty in the Beta distribution, the probability mass becomes very concentrated to both ends of the  $[0,1]$  interval when the true parameter value is close to either end of the interval. Thus, a noisy data would not get reflect as a high uncertainty parameter in the Beta-distribution but instead the mean function would follow the observations more closely, producing a zig-zag like mean function. This is, of course, an undesirable feature of the model, since the assumption is that the bias function is monotonic. Other bounded interval distributions, such as, the logit-normal distribution should be considered in the future. Also, monotonicity information should be incorporated to the Gaussian process that was used to model the bias. However, when the assumptions about the data and the experts' biases hold, the proposed method produces very promising results.

The change point models used in Article [I] and [II] have great potential for further development in terms of applying them on other fisheries related models (or for any application for that matter), or incorporating them into Bayesian stock assessment models. More interesting avenues for future research are also found in finding less computationally demanding algorithms for fitting the models. Also, to make the method more useful in more complex models, the method could be extended so that only a subset of the model parameters could experience shifts as opposed to the models used in Articles [I] and [II] where all the parameters could experience shifts. When used for S-R modelling, other models, such as, SBH and S-L used in Article [III] could also be considered, and the underlying S-R models could be extended to use environmental covariates as have been done before with time-invariant parameters (e.g., Chen and Irvine 2001).

Modelling fish reproduction, and specifically, finding stock-recruitment relationships that are useful for fisheries sciences is a demanding task (Hilborn and Walters 1992; Subbey et al. 2014). Assuming temporal variation

in the S-R model parameters in form of “recruitment regimes” as presented in Article [II] will bring fisheries scientists one step closer to completing this task. Another step into the right direction will be taken when the use of more flexible models that allow for the presence of Allee effects will become mainstream (Article [III]).

Finding better models for reproduction is not the only challenge the fisheries scientists are faced with now and in the future, however. The Greek philosopher Heraclitus of Ephesus stated somewhere around 500 BCE: “All is flux, nothing is stationary” and “Everything changes, and nothing stands still”. This realization is now maybe more evident than ever before as humanity is faced with the possibility of catastrophic climate change, irreversible destruction of vital life-supporting ecosystems, and the acidification of the oceans. All these present new and unexpected challenges also for fisheries, and the tools for detecting and adapting to change will become indispensable. Hopefully, this thesis will serve as a stepping stone for developing the necessary tools to overcome the challenges of the future in a changing world.

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