Baltic cod predation: mechanisms, impact on prey, implications for fisheries

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Abstract

Trophic interactions are fundamental in the functioning of ecosystems. Predator-prey interactions between cod (*Gadus morhua*), herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) in the Baltic Sea are typical examples of strong trophic interactions with consequences on the structure of this ecosystem. In addition to their ecological roles, cod, herring and sprat are also the main targets of the central Baltic Sea fisheries. Transition from a management based on a single species to an Ecosystem-Based Fisheries Management (EBFM), which accounts for trophic interactions, is needed to avoid overexploitation of these species and severe consequences for the ecosystem. The main aim of this thesis was to investigate ontogenetic and temporal patterns of prey selection by cod, using a unique dataset on stomach content, and to incorporate this information with various fisheries-dependent and scientific survey data, into a multispecies model with the potential to support EBFM.

Cod stomach data showed clear ontogenetic shifts in the diet, with smaller cod predating mainly on benthos and larger cod on fish (Papers I and II). The multispecies model developed and implemented in this thesis was able to represent the main patterns in the prey species and length selection by cod (Paper I). This allowed to compare prey length selection by cod and the pelagic fisheries and to evaluate the competition between them. Considerable overlap between herring and sprat lengths targeted by cod and the fisheries leads to immediate competition for the same prey. In addition, cod predates on prey sizes smaller than those targeted by the fisheries, thus generating a delayed effect of competition in the form of a loss of potential future biomass available for the fisheries. During certain periods, the loss of future biomass was estimated to be comparable to the amount of biomass suitable for fisheries directly removed by cod predation (Paper III).

A comparison of the model implemented in this thesis with two other multispecies models developed for the Baltic Sea on the same species allowed to evaluate their similarities and differences in simulated management scenarios (Paper IV and V). Despite the differences among the models, the results suggested that multi-model inference was still useful to evaluate the robustness of alternative simple fisheries management strategies to different models' assumptions, which could contribute to the development of an EBFM for the central Baltic Sea fisheries.

Keywords: predator-prey interactions, Baltic, multi-species model, size selection, EBFM, cod, herring, sprat

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Torskens predation i Östersjön: mekanismer, påverkan på bytespopulationer och implikationer för fisket

Sammanfatning

Trofiska interaktioner är fundamentala delar för ett ekosystems funktion. Predator-bytesinteraktioner mellan torsk (*Gadus morhua*), sill (*Clupea harengus*) skarpsill (*Sprattus sprattus*) i Östersjön är typexempel på starka trofiska interaktioner med påverkan på ekosystemets struktur och funktion. Torsk, sill och skarpsill har centrala roller i ekosystemet men är även viktiga målarter för fisket i Östersjön. Övergången från traditionell enartsförvaltning till ekosystembaserad fiskförvaltning (EBFF) kräver därför att trofiska interaktioner kan hanteras med avseende på arternas inbördes nivåer av exploatering och konsekvenser för ekosystemet. Den huvudsakliga målsättningen med denna avhandling är att undersöka ontogenetiska och temporala mönster i födoval hos torsk baserat på ett unikt dataset över maginnehåll. Torskens födoval kombinerades med data från vetenskaplig monitoring av fiskpopulationerna och fiskets fångster i en flerartsmodell med förutsättningar att stödja EBFF.

Maginnehållet hos torsk visade på ett tydligt ontogenetiskt skifte i torskens diet, där liten torsk i huvudsak konsumerade bentiska organismer medan större individer av torsk inkluderade en stor andel fisk i dieten (Papper I och II). Flerartsmodellen kunde återge de huvudsakliga mönstren i torskens födoval med avseende på art- och längdfördelningar i dieten (Papper I). Modellen kunde användas för att jämföra selektionen med avseende på byteslängd mellan torsk och det pelagiska fisket, och därmed förutsättningarna för konkurrens om samma byten. Ett betydande överlapp i längdfördelning av sill och skarpsill i torskens diet och fiskets fångster indikerade direkt konkurrens om samma byten. Torsk åt dessutom byten av mindre storlek än fisket, vilket orsakar en fördröjd konkurrens i form av en förlust i potentiell framtida fångst för fisket. Under vissa perioder visade modellen att förlusten av framtida potentiella fångster för fisket var av samma magnitud som den biomassa av byten som torsken konsumerade direkt (Papper III).

En jämförelse av modellen som använts i denna avhandling med två andra flerartsmodeller som utvecklats för samma fiskarter i Östersjön, möjliggjorde en utvärdering av likheter och skillnader vid olika förvaltningsscenarier (Papper IV och V). Trots skillnader mellan modellerna, så indikerade resultaten att inferens från flera modeller var användbart för att utvärdera hur robusta alternativa strategier för fiskeriförvaltning är för olika modellantaganden

Nyckelord: predator-bytesinteraktioner, Östersjön, flerartsmodeller, storleksselektion, ekosystembaserad fiskeriförvaltning, EBFF, torsk, sill, skarpsill.

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Dedication

To my family

The essence of knowledge is, having it, to use it.
Confucius

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 Kulatska*, N., Neuenfeldt, S., Beier, U., Elvarsson, B. Þ., Wennhage, H., Stefansson, G., Bartolino, V. 2019. Understanding ontogenetic and temporal variability of Eastern Baltic cod diet using a multispecies model and stomach data. Fisheries Research, 211, 338-349

II Neuenfeldt*, S., Bartolino, V., Orio, A., Andersen, K. H., Andersen, N. G., Niiranen, S., Bergström, U., Ustups, D., Kulatska, N., Casini, M. Feeding and growth of Atlantic cod (*Gadus morhua* L.) in the Eastern Baltic Sea under environmental change (under review)

III Kulatska*, N., Woods, P.J., Elvarsson, B. Þ., Beier, U., Wennhage, H., Bartolino.V. Size-selective cod predation: impact on prey, implications for pelagic fisheries (manuscript)

IV Bauer*, B., Horbowy, J., Rahikainen, M., Kulatska, N., Müller-Karulis, B., Tomczak, M. T., Bartolino, V. 2019. Model uncertainty and simulated multispecies fisheries management advice in the Baltic Sea. PlosOne

V Pope*, J.G., Bartolino, V., Kulatska, N., Bauer, B., Horbowy, J., Ribeiro, J.P.C., Sturludottir, E., Thorpe, R. 2019. Comparing the steady state results of a range of multispecies models between and across geographical areas by the use of the jacobian matrix of yield on fishing mortality rate. Fisheries Research 209, 259–270

Papers I, IV, V are reproduced with the permission of the publishers.
* Corresponding author.

The contribution of N. Kulatska to the papers included in this thesis was as follows:

I Participated in planning and designing the study. Developed the model and performed data analyses. The first author of the manuscript and handled the review process.

II Participated in data analysis and writing.

III Participated in planning and designing the study. Developed the model and performed data analyses. The first author of the manuscript.

IV Participated in planning and designing the study, data analyses, writing and in the review process. Developed the model.

V Participated in data analyses and writing. Developed the model.

1 Introduction

Predator-prey interactions are fundamental in the functioning of ecosystems (Slobodkin 1961; Odum 1971). Prey are food sources that provide a predator with the energy necessary to maintain its metabolism and all basic functions, including growth and reproduction. A predator decreases the number of prey individuals by killing them. Killed prey are usually weaker or slower individuals (Hobson 1963; Slobodkin 1968; Curio 1976; Milinski & Löwenstein 1980), thus, predators act as a force of natural selection (Darwin 1860). An effect of predation cascades down the food web. Controlling the number of its prey, the predator indirectly influences trophic interactions and species abundance at the following trophic levels, a phenomenon called trophic cascade (Paine 1980; Terborgh & Estes 2010). The crucial role of predator-prey interactions led scientists to include trophic interactions in the study of population dynamics at the beginning of the last century (Lotka 1925; Volterra 1926).

In fisheries and wildlife management, knowledge of predator-prey interactions has additional applied value. If a predator is targeted for management, some care needs to be taken to secure sufficient prey for it. If, on the other hand, a prey is targeted, some actions might be required to control its predator abundance. In cases when both a prey and a predator species are targeted, management faces even more trade-offs in order to regulate both species and sustain them on the level profitable for fisheries as well as keeping their abundance in the balance towards each other. An alternative management approach called ecosystem-based fisheries management (EBFM) was developed to account for trade-offs between different species and different objectives (FAO 1995; Pikitch *et al.* 2004). The EBFM approach takes into account non-targeted species, habitats and other elements of an ecosystem, while managing targeted species (Pikitch *et al.* 2004; Francis *et al.* 2007).

In aquatic systems, predator-prey interactions are, to a large extent, determined by the relationship between the size of predator and prey (Ursin 1973; Scharf *et al.* 2000; Mittelbach & Persson 2011). Larger predators are usually faster and more successful in catching prey (Webb 1976; Lundvall *et al*. 1999). The prey, on the other hand, may escape predation by growing in size, either to become faster (Folkvord & Hunter 1986; Lundvall *et al*. 1999), or to grow beyond the size threshold of what a predator can consume (Scharf *et al*. 2000).

Predator-prey interactions between cod (*Gadus morhua*), herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) in the Baltic Sea are well studied (Jensen 1929; Uzars 1975; Sparholt 1994), since these species are both economically and ecologically important. A wide range of multispecies models that include interactions between three species has recently been developed in the area (ICES 2005; Tomczak *et al*. 2012; Lindegren *et al*. 2014; Bauer *et al*. 2018 among others). Not all of them, however, can be used to inform EBFM, as some of them are limited to individuals or part of a population and thus do not reflect the population level of interactions, while others ignore the relation between predator and prey size and therefore do not reflect their trophic interactions realistically. The main aim of this thesis was to investigate ontogenetic and temporal patterns of prey selection by cod in the central Baltic Sea using a novel information from a unique dataset on stomach content, and to incorporate this information into a multispecies model with the potential to support EBFM.

This thesis consists of five papers (Figure 1) to reach its objectives: 1) to analyse cod stomach data and explain observed patterns of prey size and species composition in the diet, average cod prey consumption, and their ontogenetic and temporal variability (Paper I and II); 2) to develop a size-based multispecies model based on the knowledge obtained from stomach data and a multitude of other data sources (Paper I); 3) to apply the multispecies model to explore the impact of cod predation on herring and sprat, to compare prey lengths targeted by cod and fisheries and to quantify the extent of potential competition with fisheries for herring and sprat (Paper III); 4) to assess the model performance in comparison to other multispecies models and use a multi-model approach to evaluate the potential consequences of alternative fisheries management strategies (Papers IV and V).

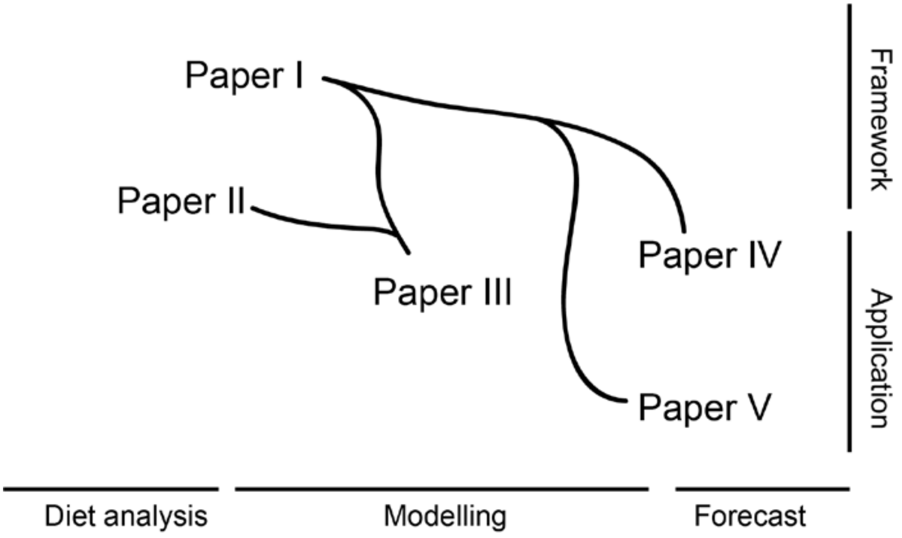

Figure 1. Links between the papers included in the thesis. Papers I and II analyse cod diet and develop framework. Papers III-V apply framework to investigate implications of cod predation for fisheries in historical time (Paper III) and in future scenarios (Paper IV and V). All papers include at least some degree of modelling.

2 Background

2.1 Ecosystem structure and predator-prey interactions

Predator-prey interactions are fundamental in the functioning of an ecosystem. Prey are food sources that provide a predator with the energy that can be used for growth or reproduction ("numerical response", Solomon 1949), which is the bottom-up effect of trophic interactions. A predator decreases the number of prey individuals by killing them ("functional response", Solomon 1949; Holling 1959), which is the top-down effect of trophic interactions. Predator reaction to changes in the prey density is characterised by two responses: functional and numerical (Solomon 1949). The numerical response is the change in the predator density due to changes in the prey density, which is achieved by the change in reproduction, survival or both (Solomon 1949), or the change in the predator aggregation around the prey (Sinclair *et al*. 2006), while the functional response is the change in the predator's consumption rate of the prey (Solomon 1949, Holling 1959), which is described as a change in the number of prey that each predator individual consume.

The prey consumed by a predator, are usually weaker or slower individuals (Hobson 1963; Slobodkin 1968; Curio 1976; Milinski & Löwenstein 1980), thus predators act as a force of natural selection (Darwin 1860). Effects of predation cascade down the food web and increase the abundance of species at the lower level of a trophic web, a phenomenon called trophic cascade (Paine 1980; Terborgh & Estes 2010). The crucial role of predator-prey interactions caught the attention of scientists, who included them in the study of population dynamics at the beginning of the last century (Lotka 1925; Volterra 1926).

Recent declines in the abundance of top predator populations, in both terrestrial and marine ecosystems, revealed that top-down effects of predation are more far-reaching than previously believed (Myers & Worm 2003; Myers *et al*. 2007; Heithaus *et al*. 2008; Baum & Worm 2009; Estes *et al*. 2011). Many striking examples are reviewed by Estes *et al*. (2011). For example, when the sea otters were present in the kelp forests they were able to control their prey – the sea urchins. As a result, density of kelps and the abundance of fish inhabiting these forests or using them as nursery grounds were high. Fish constituted a bigger part of the diet of gulls and bald eagles. Conversely, when the abundance of otters declined severely, the population of sea urchins increased, causing declines in the kelps. As a result, fish abundance declined as well, gulls switched their diet to invertebrates and eagles changed their prey preference to seabirds (Estes *et al*. 2011).

2.2 Role of size in predator-prey interactions

In aquatic systems, the relationship between the size of predator and prey is one of the main determinants of predator-prey interactions (Ursin 1973; Scharf *et al*. 2000; Juanes *et al*. 2002; Mittelbach & Persson 2011). Larger predators are usually faster and more successful in catching prey (Webb 1976; Lundvall *et al*. 1999), but this comes at increasing energy cost when pursuing prey (Schoener 1969) and increased food requirements (Murdoch 1971). Prey, on the other hand, may escape predation by growing in size, either to become faster (Folkvord & Hunter 1986; Lundvall *et al*. 1999), or to grow beyond the size threshold of what a predator can consume (Scharf *et al*. 2000). Additionally, many predators experience partition of food resources into ontogenetic niches, switching dietary preferences from one prey type to another during their life history, thereby avoiding direct intraspecific competition between different life stages (Schoener 1974; Werner & Gilliam 1984). Among fish, reaching the size required to switch to a piscivorous diet further ignites the growth of a predator and may increase its survival (Olson 1996; Mittelbach & Persson 2011).

Thus, the relationship between a predator and prey sizes determines prey selection of a predator and is fundamental knowledge for ecological modelling. In combination with quantifying the functional response (Solomon 1949; Holling 1959) and prey species selection of predator, the relationship between predator and prey sizes allows predicting predation rates based on the predator and prey abundances and their length distributions.

2.3 Stock assessment models and their limits

Acting as predators or prey, many fish species are essential for the structure and functions of ecosystems, and may also be vital for humans as a food and livelihood. Many fish stocks are overexploited today (FAO 2017). In order to recover them and prevent others from being overexploited, management action plans are developed. The initial step, however, is to know the abundance of the stock of interest. Contrary to terrestrial organisms, which often can be seen and counted, getting that information for fish in the ocean is more challenging and requires the use of analytical stock assessment models.

Stock assessment is the statistical analysis of available fisheries-related and fisheries independent data in order to estimate the current and historical status of a fish population, including abundance, mortality and productivity (Hilborn & Walters 1992). The main task of stock assessment is to provide advice on the optimal and sustainable level of fish exploitation (Sparre *et al*. 1989).

Stock assessment models can be seen as a jigsaw puzzle, where different sources of data provide their puzzle pieces, and the whole picture become apparent by combing different pieces (data) together. Sometimes a piece does not fit or maybe you just put it in a wrong place, or approached it from the wrong perspective, or something you cannot explain changed its shape. Moreover, in a jigsaw puzzle, there is a point when additional pieces do not add much to the picture; similarly, there are certain model specifications which allow an understanding of the underlying nature of the system with a little gain from the use of additional data or increased model complexity.

Many stock assessment models are age-based, they track populations separated into year-classes (cohorts). It is, however, not always possible to estimate fish age correctly. For example, there is not enough seasonal variation in tropical waters to create distinctive rings in fish otoliths, which are usually used to determine fish age (Sparre *et al*. 1989). In spite of age being more easily determined for fish from temperate waters, that is not always the case. Eastern Baltic cod is an illustrative example of that. Difficulties with estimating its age, along with major inconsistencies in data, mainly due to changes in the cod biology, were the main reasons that the analytical stock assessment of Eastern Baltic cod has not been accepted since 2014 (ICES 2014b). For species or populations where age cannot be determined length-based models are used, in which cohorts are tracked by separating fish into length groups instead of age (Sparre *et al*. 1989; Jennings *et al*. 2001). Between these two model types are age-length structured models (e.g., Stock Synthesis (Methot & Wetzel 2013); Gadget (Begley 2017)). These models take advantage of tracking annual development of age groups (as age-based models), but at the same time represent relevant functions (e.g., maturity, fisheries selectivity) as dependent on length (as length-based models). An age-length structured Stock Synthesis model (ICES 2019) was used for the Eastern Baltic cod assessment this year, which has been accepted for the first time since 2014.

Traditionally stock assessment uses single-species models. Species, however, do not live in isolation and trophic interactions will impact both predator and prey populations. For example, North Sea multispecies models showed that predation mortalities of forage (prey) fish were much higher than previously thought, depended on predator size (Ursin 1973; ICES 1984; Gislason & Helgason 1985; Pope 1991) and varied in time (ICES 1984; Gislason & Helgason 1985; Pope 1991). Ignoring predation mortality, and its variability may lead to biased estimates and projections of fish biomass and yield (Tyrrell *et al*. 2011).

2.4 Ecosystem-based fisheries management (EBFM)

The main objective of fisheries is to catch financially (commercial fishery) or nutritionally (artisanal or subsistence fishery) valuable species (Jennings *et al*. 2001). For recreational fisheries the principal values are the pleasure or trophy qualities. However, other than the choice of a gear (Jennings *et al*. 2001), the time and the place to fish, fishermen have little control of caught species. It is thus common that together with targeted species other, non-targeted, will be caught. These incidental catches may include invertebrates, fishes, marine mammals, reptiles or seabirds (Jennings *et al*. 2001). Valuable non-targeted species may be retained, while non-valuable species are usually thrown back into the sea (Jennings *et al*. 2001), often with low survival rates. Traditional fisheries management, however, is focused on single-species yield and ignores the impact of fisheries on non-targeted species.

Bottom trawling is an example of a fishing activity that has a negative impact on marine habitats, which is also overlooked by traditional fisheries management. Negative influences on sea bottoms and benthic communities are thoroughly reviewed by Jones (1992) and include, but are not limited to: scraping and ploughing, which leave distinctive marks on the bottoms, which may remain for years; sediment resuspension, which reduces light level and change nutrient availability, negatively affecting benthos and settlement of larvae; damaging or crushing shells of bivalves and crabs and breaking corals.

As a result, many habitats and ecosystems become degraded, with key species being overexploited (Pikitch *et al*. 2004; Francis *et al*. 2007). In order to restore ecosystems and to take habitats and other species into account when managing fishing, the transition to an Ecosystem-based fisheries management (EBFM) has been suggested (FAO 1995; Pikitch *et al.* 2004; Francis *et al.* 2007). The main goal of EBFM is to restore and sustain healthy marine ecosystems and to support fisheries management taking into considerations ecosystem structure, processes and functions (Pikitch *et al.* 2004; Field & Francis 2006; Long *et al.* 2015). Key principles of EBFM include considering ecosystem connections (including accounting for trophic interactions), use appropriate spatial and temporal scales, and aim for adaptive management (Long *et al.* 2015).

2.5 Multispecies models and their challenges

In spite of fisheries management and stock assessment still heavily relying on single-species models, several multi-species modelling platforms have been developed.

Plagányi (2007) defines several types of multispecies models (Figure 2) depending on their complexity and the information they account for. Model complexity ranges from extensions of single-species models with added predation (Hollowed *et al.* 2000b; Tjelmeland & Lindstrøm 2005) to whole-ecosystem models with many trophic levels included (Christensen & Walters 2004; Fulton et al. 2004). In between these two extremes is a group of Models of Intermediate Complexity (MICE, Plagányi *et al.* 2012), also called Minimally Realistic Model (MRM, Butterworth and Harwood, 1991), which include a limited number of interactions and most often commercial species (Plagányi 2007). For a more detailed review of the multispecies models, the reader is referred to the excellent works of Plagányi (2007), Hollowed *et al.* (2000a) and Jennings *et al.* (2001).

In general multi-species models used in fisheries science have three main purposes (Plagányi 2007; Plagányi *et al.* 2012):

- **conceptual** – to increase our knowledge of the ecosystem and its processes
- to test **tactical** decisions – test effects that short-term (3-5 years) management regulations (for example gear restrictions, seasonal closures, etc.) will have on the system (many of MICE/MRM)
- to test **strategical** decisions – test effects that long-term policies will have on the system (usually complex end-to-end models covering a larger part of an ecosystem)

In an attempt to make models more realistic and answer specific questions of fisheries management, developers of multispecies models face various challenges reviewed in great detail by Stefansson (2003). Here I will briefly summarise challenges that are more relevant for the models developed in this thesis.

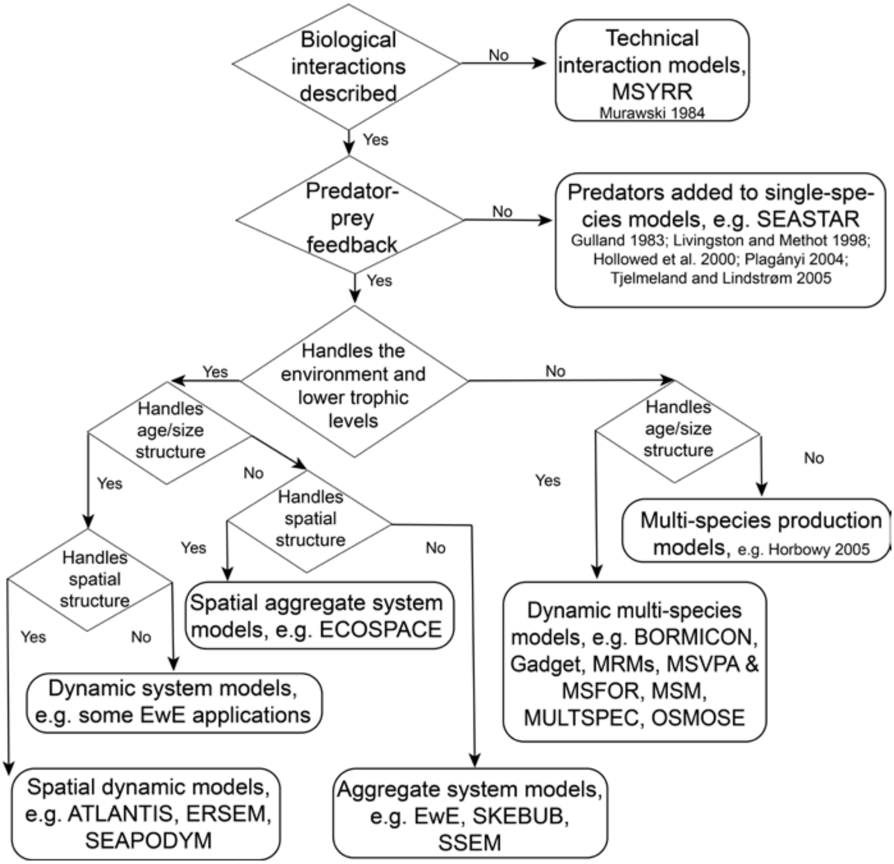

Figure2. Flowchart characterizing classification of various models. Modified from Plagányi (2007).

The appropriate **functional form** of interactions is essential for a realistic multi-species model (Stefansson 2003; Plagányi 2007). Further work on data collection and experiment, to understand mechanisms and represent feeding behaviour, is recommended (Plagányi 2007).

Combing information from **different data sources** is expected to provide a complete picture of the multiple processes and dimensions that characterize fish populations but at the cost of fitting various types of data with sometimes apparently conflicting information (Stefansson 2003). A suggested solution is weighting different sources, so more “trustworthy” sources or those to which a model is able to fit better, have a higher impact on the model estimates (Stefansson 2003; Francis 2011; Elvarsson *et al.* 2014; Punt 2017).

Traditional probability distributions, such as the Gaussian, negative binomial, multinomial or gamma distributions, are usually used as **likelihood functions** in the multispecies models (Stefansson 2003). However, they are not always appropriate. For example, length distributions (Stefansson 2003; Hrafnkelsson & Stefánsson 2004) and abundance indices (Stefansson 2003) are challenging to fit using classical multinomial or Dirichlet distributions, since they underestimate the strong intra-haul correlations between length groups. A suggested solution is to develop alternative likelihood functions which will fit the data and describe them better (Stefansson 2003).

Using multiple data sources with different likelihood functions makes it hard to impossible to apply a **goodness-of-fit test** or estimate **uncertainty** (Stefansson 2003). This is especially true for length-based models, for which approaches that work for age-based models, like Bayesian methods (Hilborn & Punt 1997; McAllister & Ianelli 1997), are not appropriate (Fournier *et al.* 2011). A spatial bootstrapping approach has been proposed as a possible solution to evaluate the uncertainty of estimated parameters, but its application remains experimental (Elvarsson *et al.* 2014).

2.6 Baltic Sea system

The Baltic Sea is a large semi-enclosed brackish water body, with pronounced salinity and temperature gradients (Elmgren 1984; Leppäkoski *et al.* 2002). Since its salinity is below levels preferred by many marine organisms and above levels preferred by freshwater organisms, few species have been able to adapt to these conditions, causing low biodiversity (Elmgren 1984; Hammer *et al.* 2008). As a result the same three species (cod, herring and sprat) are both the bulk of commercial catches (comprising together about 95% of them; ICES 2013) and the key species of the ecosystem in the Baltic Sea (Rudstam *et al.* 1994; Sparholt 1994; Lindegren *et al.* 2014).

The Baltic Sea ecosystem has gone through a sequence of reorganisations, characterised by major changes in abundance and spatial distribution of cod, herring and sprat. Under a combination of overfishing and unfavourable environmental conditions, cod abundance drastically declined at the end of the 1980s. This resulted in a predation release for sprat (one of the main prey species of cod) that, following favourable environmental conditions, sharply increased in abundance (MacKenzie & Köster 2004). Baltic Sea shifted from being a cod-dominated into a sprat-dominated (Alheit *et al.* 2005; Österblom *et al.* 2007; Casini 2013). At the same time, herring abundance decreased in a result of high fishing exploitation, degradation of spawning grounds due to eutrophication

(Casini 2013) and increased competition with sprat over main prey *Pseudocalanus acuspes* (Casini *et al.* 2010). During the 2000s spatial overlap between cod and its main fish prey species has changed: cod has concentrated mainly in the south-western part of the Baltic Sea (Eero *et al.* 2015; Bartolino *et al.* 2017), while herring and sprat densities have increased in the north-eastern part (Casini *et al.* 2011; Eero *et al.* 2012). In addition, the vertical overlap has also changed, as only a portion of sprat is found in the same part of the water column as the cod (Neuenfeldt & Beyer 2003). Furthermore, body condition of cod has declined (Eero *et al.* 2012; Casini *et al.* 2016) with potential implications for predation success, as it might be more difficult for a weaker cod to capture prey, further worsening cod body condition.

2.7 Multispecies models for the Baltic Sea

The Baltic Sea is among the most actively and systematically investigated seas in the world. It has been known for a long time that the Baltic Sea is a very fragile system, due to its harsh natural conditions and low biodiversity. That, together with sharing Baltic resources, was the reason for a close co-operation between coastal countries to monitor the state of it, in order to protect it (Leppäranta & Myrberg 2009). The crucial role of interactions between Baltic Sea species on their dynamics also has a long history of studies (Jensen 1929; Uzars 1975; Sparholt 1994).

The long tradition of multispecies modelling in the Baltic Sea is reflected in a wide range of models, which span across a broad gradient of applications from tactical (testing short- to medium-term consequences of management actions) to strategic (testing long-term consequences of, e.g. policies). Many include trophic interactions between cod, herring and sprat in the central Baltic, with marked differences in their approach to species interactions. Tactical models include the Stochastic multispecies model (SMS, ICES 2012) and the Multispecies virtual population analysis (MSVPA, ICES 2005). Both account for the prey species preference and average daily ration of cod. However, both SMS and MSVPA are age-structured models and do not account for prey length preference of cod. A simplified approach is applied by Multispecies production model (MSPM, Horbowy 2005) where age groups of all species are replaced with life stages. For all these three models, consumption is parametrised using stomach data from a database with a very limited temporal and spatial coverage.

Implementations of more strategic models for the central Baltic Sea include Ecopath with Ecosim (EwE; Tomczak *et al.* 2012; Bauer *et al.* 2018) and more recently Atlantis (Bossier *et al.* 2018). Contrary to age-structured models, EwE simplifies the modelled populations into few life-stages, and trophic interaction is based on the “foraging arena” theory (Walters & Juanes 1993; Ahrens *et al.* 2012) where the vulnerability of prey populations to predation is related to spatial and temporal restrictions of prey and predator activities. The predation parameters of the EwE model used for the integrated assessment of the Baltic Sea (ICES 2016) were also derived from a sparse, old set of cod stomach data. That model was recently re-parameterized using the newly compiled database of cod stomachs (same as used in this thesis), but the model was limited to the period 2004-2013 (Bauer *et al.* 2018). The Atlantis model uses a mechanistic approach to trophic interaction, where predator consumption depends on prey availability parameter and various predator characteristics, such as growth and consumption rate, gape size, functional response. However, dietary patterns in the Atlantis model for the Baltic Sea (Bossier *et al.* 2018) were informed by SMS and EwE.

3 Stomach data analysis

Stomach content data are among the most relevant direct observations of species trophic interactions and provide prey species-specific information about the predator diet in the wild. However, individual stomach content is a snapshot of what that individual predator has eaten recently, with detection probability of different prey items influenced by their digestion rate. Nevertheless, sufficient sample size, its spatial and temporal coverage, can compensate for that and provide a realistic picture of predator’s diet.

A comprehensive dataset of cod stomach data from the Baltic Sea for the period 1964-2014 (Figure 3) has been recently prepared under the EU tender No MARE/2012/02 and made available by ICES (Huwer *et al.* 2014; ICES 2014c). Data were collected during various national sampling programs by Baltic countries and during the Baltic international trawl survey (BITS, ICES 2014a). This cod stomach dataset is a central information source in my thesis and was used directly to analyse the cod diet and to estimate consumption (Papers I and II) and predation parameters (values that characterise cod prey selection) in the models (Papers I, III-V).

With the analysis of stomach data, I explored the temporal and ontogenetic variability of three aspects of the cod diet: average daily consumption, species composition and prey size selection. I compared diet compositions in the periods of major changes in the Baltic system: 1) 1974-1989, prior to the ecosystem shift, which is characterised by high cod and herring abundances and low sprat abundance (Möllmann *et al.* 2004; Alheit *et al.* 2005; Casini 2013); 2) 1989-2007, when cod and herring populations declined and sprat increased; and 3) 2007-2013, when the cod population increased but was concentrated in the Southern Baltic Sea (Eero *et al.* 2012).

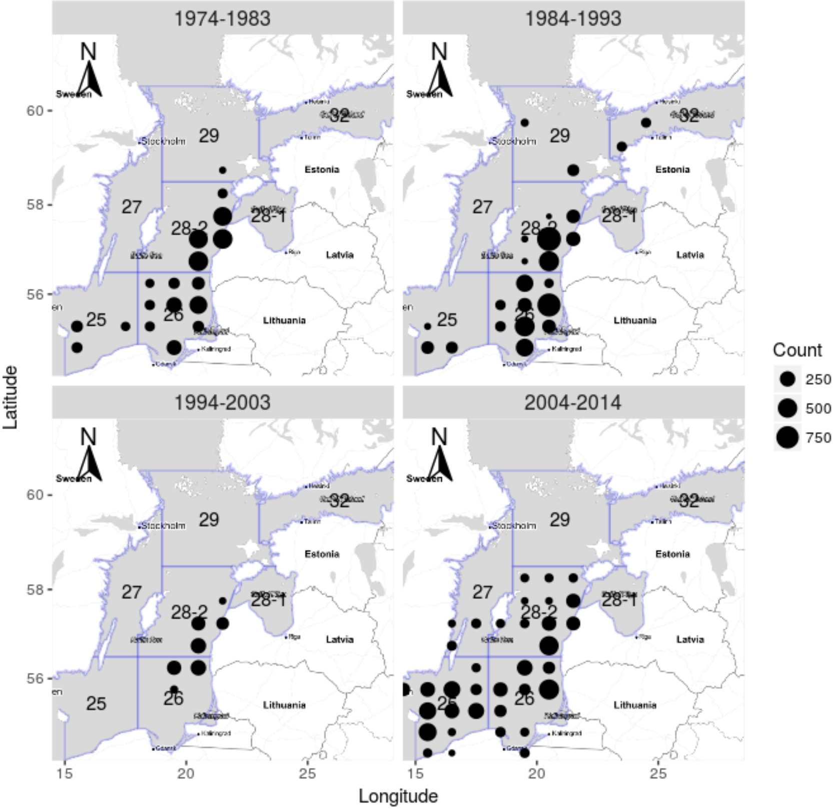

Figure3. Spatio-temporal distribution of cod stomach samples in Quarter 1. The size of the circles corresponds to the sample size, while location corresponds to the centre of the ICES rectangle (ICES 1977), where the sample was taken. Numbers 25-32 are ICES sub-divisions (ICES 1969).

Stomach data of Baltic cod show clear ontogenetic shifts (Figure 4), with smaller cod feeding mainly on benthos (saduria and mysids) and larger cod being piscivorous and feeding mainly on herring and sprat (Paper I and II). Even though proportions of both mysids and saduria in cod diet decline with cod growth, saduria remains an important prey item throughout whole cod ontogeny and even increase in the diet of cod that reach 60 cm (Figure 4; Paper I and II). Sprat becomes an important prey item for cod at a smaller size than herring does (ca. 30 cm vs. ca. 35 cm; Figure 4). Cod diet has a seasonal pattern: in the first half of the year, cod feeds mainly on sprat, while in the second mainly on herring and benthos (Paper I, Uzars 1975). Changes in the prey abundances are reflected in the cod diet composition, with sprat proportions being lower in 1974-1988, when sprat abundance was lower, and benthos proportions being lower in 2007-2013, when benthos abundance is considered to be drastically declined due to increase in hypoxic areas (Figure 4, Paper I).

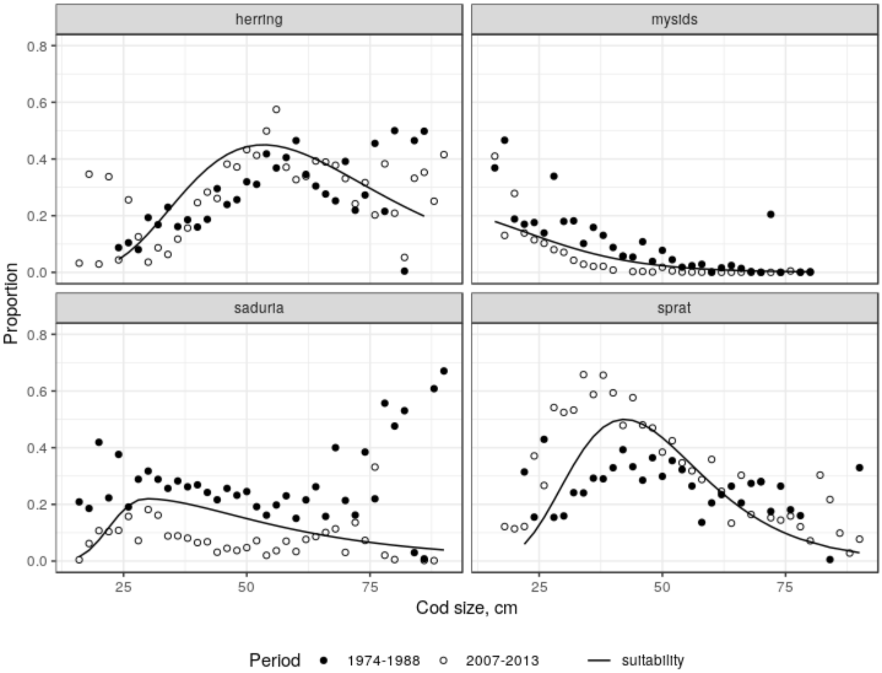

Figure4. Proportional contribution in weight of different prey items in the cod stomachs (points) in relation to cod size with suitability functions, describing prey selection by cod (lines) fitted to them (see Box 2, Section 4).

Analysis of prey length composition of cod diet showed that size ranges of herring and sprat, observed in the cod diet, overlap, with the degree of overlap depending mainly on the size of cod. For example, the highest proportion in the diet of 35-60 cm cod constitutes of 10 cm sprat and 15-16 cm herring.

Stomach data represent the consumption several hours prior to the time when stomach samples were taken. In order to infer about predator’s daily rations, stomach data need to be converted using an evacuation model or a bioenergetic model (Hansson *et al.* 1996). Several of these models were developed for cod from different regions. In the Paper I, the model of evacuation rate (*R*) developed by (Jones 1978) in an experimental setting with the North Sea and Faroe cod (Box1, Figure 4) was used, while in the Paper II – the cylinder evacuation model proposed by Andersen (2012) (Box 1). The two models are rather similar. Major difference is how prey energy density is accounted for and that Jones model was initially parametrised on the North Sea and Faroe cod (Jones 1978), while the cylinder model was parametrised on cod caught at the Danish coast of Skagerrak. When compared under 8° temperature, for cod with length 35 cm eating 5.5 g prey, with prey energy density 1 kJ/g (so both models represent consumption in weight), models differed by less than 10%.

Box 1: Evacuation and bioenergetics models

Jones (1978) evacuation model:

$$R = 24Q\left(\frac{L}{40}\right)^{1.4} EW^{0.46},$$

where R is consumption rate (kJ/day), L is the cod length and W is the weight of its stomach content, $(L/40)^{1.4}$ is length correction, $W^{0.46}$ is weight correction, E is prey energy density (kJ/g; it was assumed to be equal 1 kJ/g to estimate consumption rate in g); Q is digestion coefficient and = 0.16 at temperature 8°, 24 is the number of hours in a day.

Cylinder evacuation model (Andersen 2012):

$$R = 24\,\rho_0 L^{1.3} e^{0.083T} E^{0.15} \sqrt{W}$$

where R is consumption rate (kJ/day), E denotes the average energy densities (kJ/g) of the individually observed total stomach contents W (g) of cod with length L (cm) and the basic evacuation rate parameter $\rho_0 = 2.43 \times 10^{-3}$.

Daily consumption reconstructed using evacuation models (Figure 5) showed an exponential relation to cod length. Estimates of average consumption (Paper I and for 5 year periods in Paper III) derived in my study from the Baltic cod stomachs are comparable to the values used by similar multispecies models from the other areas, with cod as a predator (Figure 5).

In Paper II cod feeding level was estimated as the ratio between maximum consumption and daily consumption. Feeding level of small (20-30 cm) cod decreased a lot during the last decades and reached the minimum in 2005-2014. The low feeding level means that this group of cod does not consume a sufficient amount of prey. This can slow down the growth of this group, impeding the critical transition to a piscivorous diet, decreasing cod condition and survival (Olson 1996; Mittelbach & Persson 2011). This likely creates a bottleneck for the cod population (Paper II).

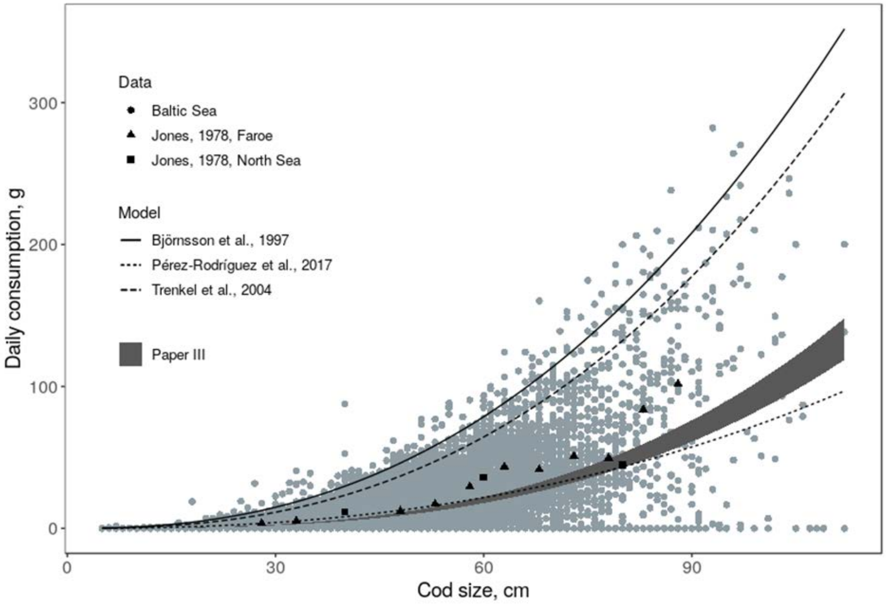

Figure5. Estimation of average consumption (line) as a function of cod size, based on daily consumption (points) reconstructed by evacuation rate model from content of individual cod stomachs. Data points with daily consumption of 0 g are empty stomachs, while those above 0 g contain food. Other point types represent evacuation rates from laboratory experiments carried on by Jones (1978). Other lines compare model estimates to similar cod models, where Pérez-Rodríguez *et al.* (2017) and Paper III used average consumption while Björnsson *et al.* (1997) and Trenkel *et al.* (2004) used maximum consumption. Consumption, in the models of Pérez-Rodríguez *et al.* (2017) and Björnsson *et al.* (1997), was dependent on temperature, which was set to 8 °C and 2 °C, respectively.

4 Developing a multi-species model using knowledge from stomach data

To reconstruct population dynamics of cod, herring and sprat, their trophic interactions and the effect of fisheries, an age-length structured model using Gadget (Globally applicable Area Disaggregated General Ecosystem Toolbox) was built. Gadget models represent biological processes like growth, maturation, reproduction, consumption, etc. in the form of functions, which are often length-based, and also the interaction between various components of the ecosystem, such as, predator-prey interactions, the impact of environment and fisheries (Begley 2017; see also Taylor & Stefansson 2004; Trenkel *et al.* 2004; Pérez-Rodríguez *et al.* 2017 for multispecies model examples). In addition models can be built as multi-area, to account for differences in the spatial patterns; and multi-fleet, to account for differences in the fish selection by and availability for various fleet segments. I developed a single-area multi-fleet model that includes sprat, herring, cod active (mainly bottom trawl) and cod passive (mainly gill-nets) fleets.

Modelling process in Gadget can be outlined as three steps:

1. provided with initial parameter values, Gadget runs a forward projection model;

2. obtained predictions are compared to the observed values in order to calculate likelihood scores (negative log-likelihood) and represent goodness of fit;

3. Gadget re-adjusts parameter values and re-runs the model until optimum parameter values are found, which produce the overall best fit of the model to multiple data components (Begley, 2017).

The model used 21 datasets to estimate the parameters (see Paper I, Supplementary material, Table A2). The nature of these datasets is different (length distribution, survey indices, diet composition, etc.), thus, an appropriate function for each data type (called likelihood component) is used to calculate the model fitting in the form of a likelihood score during the optimization. For most datasets likelihood was estimated as a sum of squared errors. Scores of individual likelihood components are then combined into an overall likelihood score, also referred to as an objective function, which the optimization algorithm tries to minimise by estimation of optimal parameters' values (Begley 2017).

Gadget uses three optimization algorithms run in a sequence: first, a wide area search simulated annealing (Corana *et al.* 1987) to reach the general area of a solution, followed by a local search Hooke and Jeeves algorithm (Hooke & Jeeves 1961) to rapidly find a local solution and then Boyden-Fletcher-Goldfarb-Shanno algorithm (BFGS, Bertsekas 1999) to fine-tune the optimization. This procedure is repeated several times to prevent converging to a local optimum.

In order to prevent some likelihood components from dominating the objective function and reduce the impact of low quality data iterative re-weighting was used, which assigned the inverse variance of the fitted residuals as component weights.

Models with many parameters (e.g. multi-species model implanted in this thesis included about 300 parameters), which may be correlated, make difficult to discriminate between different possible combinations of estimated values. In addition, models of different species usually differ in their structure and data sources that they use, which sometimes include conflicting information. These challenges caused the model to be built in a several step approach.

The model implementation started with the parametrisation of single-species models for cod, herring and sprat (see Paper I, Supplementary material, Table A2 for a summary of data sources used in the models, and Table A3 for parameter values). This step simplifies the model, decreases the number of data sets and estimated parameters, compared to the direct multi-species implementation. This helps to evaluate which parameters are correlated and thus need to be estimated in different runs, which data-sets provide conflicting information, to which data-sets model fits better; and it simplifies assigning a weight to each of data sets. Goodness of fit of each single-species model was based on visual inspection of the model fitting (whether predicted values had a similar magnitude and trends as observed values) and by estimating overall and individual components likelihood scores.

When satisfactory single-species models were parametrised, they have been linked into a multi-species implementation with cod feeding on both herring and sprat. In addition to herring and sprat, which are dynamically represented in the model, saduria and mysids, which are important prey items for cod, were added to the model with constant biomass (little is known about actual values and trends of their biomass in the Baltic). In addition, a generic group, “other food”, was added as a constant prey. This category includes other species (besides herring, sprat, mysids and saduria) that cod consumes and ensures that cod always has prey available to fulfil its food requirements without overconsumption of sprat and herring.

Some of the parameters in the multispecies model were fixed to the values estimated during the single-species step (e.g. growth and fishery selectivity parameters of all species), while others were estimated. From the estimated parameters, some used output of single-species implementation as initial values (e.g. annual recruitment of herring and sprat), while others were typical to the multi-species implementations (e.g. parameters of prey preference for cod) and their initial values were found in the literature (e.g. laboratory experiments, similar multi-species models) or estimated outside the model. Functions to describe prey species and size preference of cod (suitability; see the next page for Box 2) were chosen based on patterns of the species composition observed in the stomach data (Figure 4).

The model, fitted to prey species and length composition in the stomach data, was able to represent the general ontogenetic shifts in the predicted cod diet. The proportion of clupeids in the predicted cod diet increased with cod growth and eventually declined when cod reached more than 80 cm in length, while the proportion of mysids and saduria progressively declined. However, the model systematically underestimated the ratio of herring in the diet of all size groups of cod and sprat in the diet of smaller cod (< 35cm) but overestimated the ratio of sprat in the diet of larger cod (> 35 cm). The proportion of sprat slightly increased with time, while the proportion of herring was highest during 1974-1988, when cod and herring abundances were high and sprat abundance was low (Paper I).

Temporal patterns observed in the diet composition from the stomach data were better represented by the model for the 1974–1988, when cod was more abundant and more stomachs were sampled. In the period 1989-2006, the model predicted an overall decrease in the proportion of herring in the diet of cod, which reflected the decline in the abundance of this prey. On the contrary, the stomach data showed an increase in the proportion of herring in the diet of 35-80 cm cod during this period, which remains unexplained. The spatial and temporal scales that link the prey population size to its local densities and to the predator-prey encounter remain unclear, and the model ignores possible changes in the horizontal and vertical overlap between cod and herring, which may have affected the interactions between them. Moreover, it is important to note that cod stomachs were poorly sampled during the 1990s until the mid-2000s and biases in the data cannot be excluded during this period (Paper I).

Box 2: Predation in Gadget

Consumption

Consumption of each prey in the model was a function of both predator (L) and prey length (l), and related to prey availability, predator food requirements and preference for the different prey as follows:

$$C_p(l,L) = \frac{N_L M_L S B_{p,l}}{\sum_{preys} S B_{p,l}}$$

where B is biomass of prey species p and length l, S is suitability function, which estimated the probability that the prey would be caught by the predator based on the lengths of predator (L) and prey (l). $\sum_{prey} pSBp,_{l}$ is the total biomass of all suitable prey, M_L is the average consumption for the predator of length (L) to satisfy its dietary requirements, and N_L the number of predator individuals of that length.

Suitability functions (in all the functions the parameter *d* was used to represent the prey species preference by cod):

An **exponential suitability function**, which logarithmically depends on the size of the predator (L), was used to represent the selection of mysids:

$$S(L) = \frac{d\delta}{1 + e^{(-\alpha-\gamma L)}}$$

The **Andersen-Ursin suitability function** (Ursin 1973; Andersen & Ursin 1977), where suitability depends on the ratio between predator (L) and prey (l) lengths, was used to represent the selection of saduria (prey length was constant), herring and sprat:

$$S(l,L) = \begin{cases} de^{-\frac{\left(\ln\frac{L}{l}-p_1\right)^2}{p_4}}, \; if \ln\frac{L}{l} \le p_1 \\ de^{-\frac{\left(\ln\frac{L}{l}-p_1\right)^2}{p_3}}, \; if \ln\frac{L}{l} > p_1 \end{cases}$$

In case of sprat and herring p_3 were assumed to be equal p_4, i.e. suitability curves were symmetric.

A **constant suitability** function was used to represent the selection of “other food” as it is independent on both the sizes of predator and prey:

$$S(L) = d$$

5 Application of the multispecies model

Targeting the same prey makes competition between humans and predators unavoidable. Size ranges of prey that predators predate on are often limited, and may or may not overlap with size ranges targeted by fisheries. When they do overlap, the effect of competition with fishery over that prey is immediate and affects both the predator and fisheries. However, if the predator consumes the same prey species as the fishery but targets smaller prey sizes, the effect of the competition will be delayed, since predation on smaller sizes may result in a potential loss of future fishing opportunities targeting larger sizes. Conversely, when the fishery targets smaller individuals than the predator, a delayed effect of competition affects the predator. The delayed effect of competition affects only the competitor that targets larger fish.

I found both immediate and delayed effects of competition between cod and the pelagic fisheries in the central Baltic Sea. The immediate effect of competition was generated by the considerable overlap between prey lengths targeted by cod and fisheries (about 40% size overlap for herring and 55% for sprat). Moreover, the overlap was largest in the 1974-1988 when cod population abundance was high and the represented by many large individuals, and gradually decreased with time (Paper III).

Cod often consumes smaller clupeids than those targeted by the fisheries. This generates a delayed effect of competition which was quantified by calculating how much of the prey biomass consumed by cod below the harvestable size, would have become available for the fisheries later in time. The estimated prey biomass unavailable for fisheries due to a delayed effect of cod consumption (Figure 6) was often similar to that due to an immediate effect, doubling the total effect of potential competition with cod (Paper III).

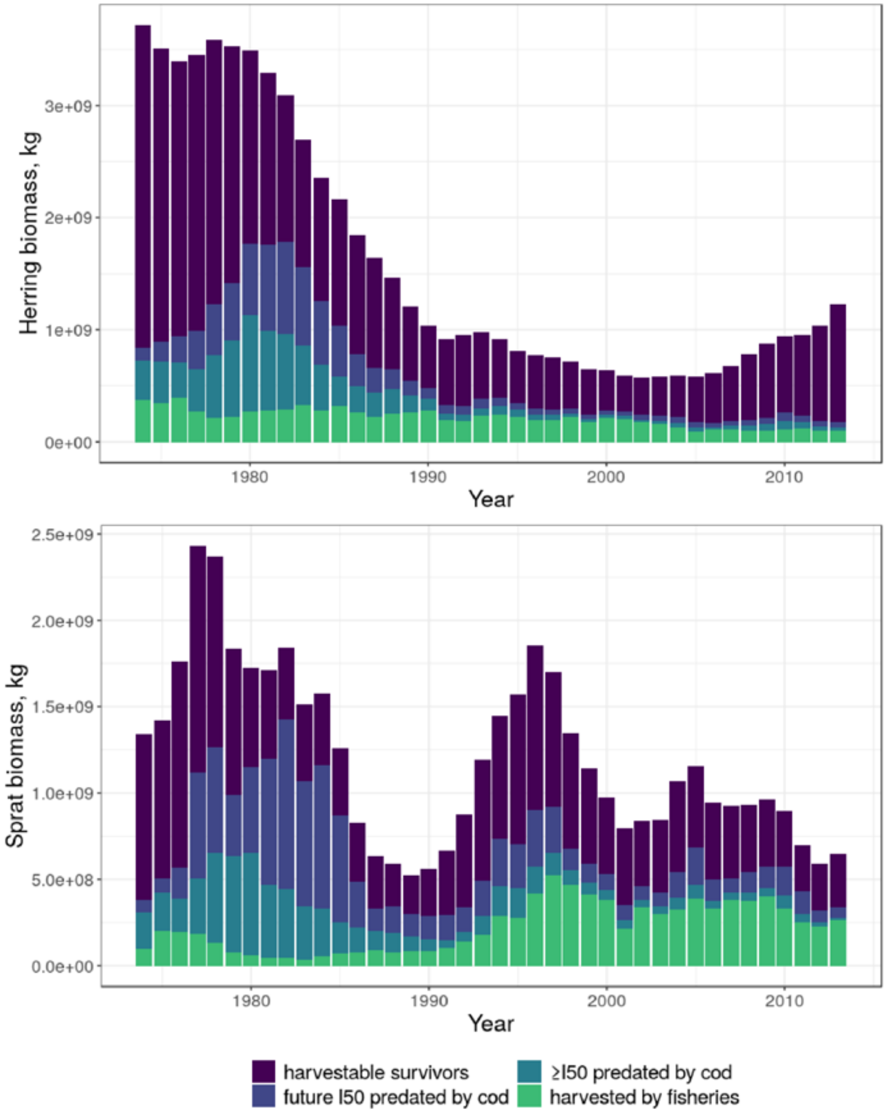

Figure6. Temporal variability in the potential competition between cod and fisheries for herring (upper panel) and sprat (lower panel) from a fisheries perspective. Biomass harvested by the fishery is compared to the biomass of prey with a size $\geq l_{50}$ (i.e. harvestable size by fisheries) which is consumed by cod (i.e. immediate effect of competition with cod), and the biomass of prey at l_{50}, to which $< l_{50}$ consumed prey would have grown in the absence of cod (i.e. delayed effect of competition with cod). The biomasses of herring and sprat of harvestable for fisheries size that survived until the end of the year, i.e. after all predation and harvesting events, are also shown for comparison.

6 Multi-model inference to support EBFM

Multispecies models are complex and challenging to implement and to understand and communicate their output. In addition, they may have certain degree of uncertainty, especially due to biases, assumptions and limitations. If a management strategy is evaluated by a single model, a risk to reach misleading conclusions exists due to model uncertainty. If a strategy instead is evaluated and supported by multiple models its robustness will be higher. This can be done in a similar manner as several global climate models are routinely compared to generate future climate scenarios (IPCC 2007; Moss *et al.* 2010) or several species distribution models are compared to support conservation planning (Jones-Farrand *et al.* 2011).

Three multispecies models (Box 3): Globally applicable Area-Disaggregated General Ecosystem Toolbox (Gadget, implemented in this thesis), Ecopath with Ecosim (EwE) and a multispecies stock production model (MSPM); were compared in the multi-model context using two approaches. Models were built in the framework of a common project – MareFrame and used similar datasets to minimise differences due to data used.

In the first approach (Paper IV), the impact of model uncertainty (differences in the model based on their structure) on the management advice (here and in the following text I use this term to describe suggested changes to fishing mortalities in order to achieve specific management goal) to five alternative management strategies (Table 1) was examined. The strategies differed in their objectives, which were discussed and prioritised during meetings with several stakeholder groups. Some objectives were economy-oriented, i.e., maximizing the profit of different fisheries segments (i.e., pelagic, targeting herring and sprat, and demersal fisheries, targeting cod), while others were conservation-oriented, i.e., the recovery of the cod population. Subsequently, we investigated the medium-term performances (18 years) of the models in alternative management scenarios in terms of indicators describing relative changes in spawning stock biomass (SSB), catch and profit compared to the levels in 2011-2013 (Paper IV).

Box 3: Model description

Ecopath with Ecosim (EwE; is a commonly used software and process-based modelling approach to study whole-ecosystem effects of fisheries. The EwE model of the open Baltic Sea includes charismatic species such as grey seals and offshore fish-feeding birds, four fish species (cod, herring, sprat and flounder), the benthic part of the food web, four zooplankton groups and one phytoplankton group. The Ecopath component represents biomass flows among organismal groups within the food web and to fisheries in the ‘model year’, 2004. Ecosim dynamically simulates the temporal development of biomasses and catches in the system 2004-2013 given certain fishing mortalities (defined as yearly harvest rate, catch/biomass) and environmental forcing. Seal predation on cod, herring and sprat was described by saturating function of seal biomass and linear function of prey biomass. EwE model simulations have been carried out using the software Ecopath with Ecosim.

Gadget is a platform to run statistical models of marine ecosystems consisting of a limited number of species, accounting for biological processes, such as maturation, growth, predation, etc. (Begley 2017). The Gadget implementation in the Baltic is a multispecies and multifleet model. Trophic interactions are represented by cod feeding on both herring and sprat, as well as on benthic prey. Seals are represented in the model as a fleet, with each seal consuming 5 kg fish/day with a constant proportion of cod, herring and sprat. Total seal consumption is thus a linear function of seal abundance. Inclusion of seals is the major difference of the model formulation compared to the one developed in the Paper I (and described in the section 4 of this thesis). The model is age-length structured with quarterly time steps running from 1974 to 2013. The current implementation uses the package Rgadget for R.

The MultiSpecies Production Model (MSPM) is a simplification of the age-structured multispecies model. The model was applied to simulate stock dynamics in yearly time steps and interactions of the cod, herring, and sprat stocks in the central Baltic from 1982 to 2013. It considers the trophic interactions among these stocks (predation of cod on herring, sprat, and young cod), the environmental impact on the growth of cod and herring and density-dependent growth of sprat. Predation in the model depends on the biomass of available food, thus cod cannibalism is dependent on clupeid biomass. Model simulations were run using Excel with VisualBasic.

Table 1. ***Alternative management scenarios.*** *Fishing mortality (F) values were individually selected in each model according to the objectives of each scenario, except for the 'Status Quo' scenario which represents a continuation of current practices.* P_i *values represent yearly discounted profits to net present value from fisheries on stock i,* B_i *annual biomasses and* SSB_i *spawning stock biomasses of stock i, where the subscripts c, h and s refer to cod, herring and sprat, respectively.*

Scenario		Objective
Piscivore Exploitation (PE)	Maximize summed cumulative discounted profit of bottom trawlers (BT) and gillnetters (GN) based on their cod catches.	$\boldsymbol{max \sum_{y=2014}^{y=2032} P_c}$
Forage Fish Exploitation (FE)	Maximize cumulative discounted profit of pelagic trawlers (PT) based on their herring and sprat catches	$\boldsymbol{max \sum_{y=2014}^{y=2032} (P_h + P_s)}$
Portfolio Fishery (PF)	Maximize cumulative discounted total fisheries profits.	$\boldsymbol{max \sum_{y=2014}^{y=2032} P_{c,h,s}}$
Piscivore Recovery (PR)	Maximize cod biomass compared to clupeids with constraint keeping herring and sprat at viable levels	$\boldsymbol{\max(\overline{\frac{B_c}{B_s + B_h}})_{2028}^{2032},}$ $\boldsymbol{\overline{SSB_h}_{2028}^{2032} > B_{lim,h}}$ $\boldsymbol{\overline{SSB_s}_{2028}^{2032} > B_{lim,s}}$
Status Quo (SQ)	Fs set to average of the last three years' (2011-2013) values in model hindcast	

In many cases, the models deliver consistent answers on how to adjust fishing mortality rates to reach a specific objective. This consistency is highly relevant for the potential to support EBFM. Advice on the scenarios aiming to maximize profits of the pelagic fishery ('Forage Fish Exploitation') or the total fishery ('Portfolio Fishery') had higher degree of model agreement (Figure 7) than those maximizing profits of the demersal fishery ('Piscivore Exploitation') or those related to a desired fish community composition ('Piscivore Recovery'), as model differed on the feedback mechanisms between prey and cod (Paper IV).

In the second multi-model approach (Paper V) multispecies models were run to equilibrium under a small change (±10%) of status quo fishing mortality (level of 2011-2013). Estimated yields at equilibrium of all species under all possible combinations of fishing mortality were used to estimate the elements of the

Jacobian matrix. The elements show the direction of change of each species yield due to change of its fishing mortality. The Jacobians were also used to evaluate the importance of multi-species effects for each species, i.e., how the yield of a specific species is affected by the change in a fishing mortality of another species. The values estimated by the models were then compared (Paper V).

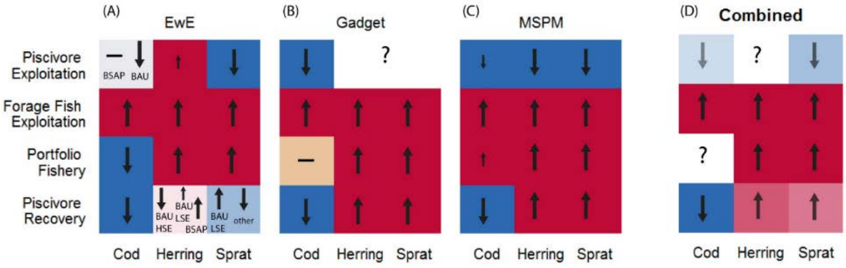

Figure7. Required increases (upward arrows, red tiles), decreases (downward arrows, blue tiles) by 10–20% (small arrows) or more (large arrows), or no change (hyphen, beige tiles) compared to Status Quo Fs to achieve objectives of each management scenario according to each model (A-C) and combined (D). Lighter tiles indicate uncertainty in advice. In (A) they indicate cases when the advice provided by EwE on F was sensitive to the environmental scenario. In (D) light tiles indicate model differences in the combined information from (A)-(C). White tiles (question mark) represent cases when the model does not inform about Fs maximizing scenario objectives (B) or completely contradictory information from the model ensemble (D). BSAP indicates 'Baltic Sea Action Plan', BAU 'Business-As-Usual', HSE 'high seal growth' (10% growth rate) and LSE 'low seal growth' (5% growth rate) scenarios. 'Other' in (A) refers to all other scenario combinations except of BAU-LSE.

All three models showed weak multispecies effects of clupeid fishing mortality on cod (it was impossible to evaluate this effect for Gadget since the model does not account for bottom-up effect of clupeids on cod) and somewhat stronger effects of cod on herring and sprat, with Gadget and EwE showing stronger effect than MSPM. The effect of change in a cod fishing mortality on herring yields was stronger than on sprat yields. Models are also consistent in the direction of yield change of each species due to change in its fishing mortality, except for the Gadget result on cod, which showed a decrease of cod yield due to further increase in its fishing mortality, while other models suggested an increase of yield.

The Jacobian matrix is a useful approach for comparing different multispecies fisheries model due to its simplicity. Investigation of a models behaviour using this approach is beneficial if the task is to answer only one or two simple questions and it uses a clear method of analysis of model results to address these questions. While the Jacobian matrix approach seems an excellent analysis for investigating the near field responses of long term yield or biomass of models to relative changes in mortality rate it is clear that other analytical approaches will be needed to compare for example the ecosystem structure and functions that particular models propose or to consider the trajectories that stocks might follow on the path to any long term steady state (Paper V).

Due to model uncertainty of individual models, ensemble modelling can become an important and necessary approach to operationalize multispecies advice and support EBFM. However, an initial step toward ensemble modelling is a comparison of the output of different models, which will improve understanding of their differences. Comparing multiple models using performance indicators, i.e., spawning stock biomass (SSB), yield and profit (Paper IV) or Jacobian matrices (Paper V), may be an important step toward operational EBFM and for the support of current stock assessment (Pope 1991; ICES 2018).

7 Conclusions

To summarise, in my thesis I explored cod stomach data and found clear ontogenetic shifts in cod diet, with smaller cod predating to a large extent on benthos, while larger cod being mainly piscivorous (Papers I and II). Feeding level (ratio between the maximum and realised consumption) of smaller cod has decreased in the recent years. It has likely contributed to a decline in growth and created a potential bottleneck for the cod population at the juvenile stage (Paper II). Stomach data were used to estimate prey species and length selection by cod and its food requirement in the model (Paper I). The model implemented in this thesis was able to represent main ontogenetic and, to some extent, temporal patterns in the prey species and length selection by cod (Paper I). This allowed to compare the prey length selection of cod and the pelagic fisheries and to evaluate their potential competition. Considerable overlap between targeted herring and sprat lengths by cod and the fisheries leads to direct competition for the same prey. In addition, cod has also a high preference for prey size smaller than those targeted by the fisheries. This results in a loss of potential future biomass available for fisheries, since those prey would have grown into harvestable sizes if not predated by cod. In some years the immediate and the delayed effects of competition with cod were of similar magnitude, doubling the total effect of potential competition with cod (Paper III).

Comparison of the model with two other multispecies models, developed for the Baltic Sea on the same species, in a framework of a common project – MareFrame, allowed to evaluate their similarities using performance indicators (Paper IV) and Jacobian matrices (Paper V). This multi-model inference may be useful to inform and support EBFM, since it allows to evaluate the robustness of alternative fishery management strategies to assumptions and uncertainties of the models.

8 Future perspectives

The multispecies model in the core of my thesis, describes major patterns of cod predation using a whole-population scale. The model has a potential to support further applications, such as, in depth analysis of cod-clupeid interactions in the central Baltic Sea, and evaluating tactical, i.e. the short and medium-term consequences of alternative fishing regimes or gear regulations on the dynamics of the system; as well as strategic decisions, i.e. the long-term consequences of specific policies. I would like to outline some potential further modifications and improvements to the model.

A decline in the cod abundance and a drastic decrease of the cod condition in the Baltic Sea (Eero *et al*. 2015; Casini *et al*. 2016), have called for more actions and for updating existing action plans (EU 2016) to recover the eastern Baltic cod stock. The pinnacle of these measures has been the recent zero catch precautionary advice given by ICES for this stock (ICES 2019) and cod fishing ban in Southern Baltic (EC 2019). My model could be readily applied to predict the consequences of a cod recovery plan for the populations of herring and sprat and implications for the fisheries. For this, the model would only require an update with the inclusion of the most recent years of data (currently the model runs to 2013). Such update is currently scheduled for the Autumn 2019 to present the model at the Working Group on Multispecies Assessment Methods (WGSAM).

At the moment the model only accounts for the top-down effect of trophic interactions. This was in order to decrease the complexity of the model, to reduce the need of too many assumptions on aspects where knowledge is still lacking; and to break the issue of trophic interaction into smaller specific aspects suitable to focus on in a thesis. In order to explore the bottom-up effects of prey on cod as well as the energetic trade-offs of cod for selecting one prey over another, cod growth needs to be linked to consumption.

The spatial distribution of cod has considerably contracted south-west towards the central Baltic and Bornholm Basin during the 1990s and 2000s (Eero *et al*. 2012; Bartolino *et al*. 2017). At the same time, the distribution of both herring and sprat have shifted in the opposite direction towards the north-east

(Casini *et al*. 2011; Eero *et al*. 2012) generating a possible spatial mismatch between cod and its prey which may have significant consequences on their trophic interactions. In the earlier stages of my PhD project, I have built a multi-area model, but I found that the survey indices alone were insufficient to parametrise a migration matrix to represent movement between the different areas and an additional information on fish movement from tagging or other sources was necessary. Recent accomplishments in the projects TABACOD (digitalisation of historical tagging, Mion) and BONUS-Inspire (reconstructing cod spatial distribution from survey data and environmental variables, Orio 2019) may provide the necessary data and knowledge to implement a simple multi-area model which could be used to investigate the implications of a variable spatial overlap between cod, herring and sprat.

The population of grey seals (*Halichoerus grypus*) in the Baltic Sea has increased during the last 30 years from about 3 000 individuals in the 1970th (Harding & Härkönen 1999) to 30 300 in 2017 (Luke 2017). HELCOM experts, however, indicate that flight counts represent only about 60-80% of the actual seal population (Härkönen 2016), meaning that the current grey seal population may include 34 000-50 000 individuals. Cod, herring and sprat are among the top-five prey species of seal pups diet and in the top-three of juvenile and adult seal diet in the central Baltic (Lundström *et al*. 2010). This means that increasing seal populations would contribute to increasing mortality of cod, herring and sprat. Seal predation was accounted for in the model presented in Paper IV by a simple representation of “seal as a fleet”. In this case, the prey biomass consumed by seals was linearly related to the seal population size and proportional contribution of herring, sprat and cod to the seal prey biomass was constant in time and based on a limited number of seal stomachs and intestines collected during 2001-2005 (Lundström *et al*. 2010). A better understanding of seal consumption and temporal variability of seal diet based on a larger and more representative stomach sampling would be required to provide more realistic estimates of seal predation. In that direction, further developments could include the implementation of a dynamic seal model to be included within the current framework.

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Popular science summary

Marine resources provide a multitude of various values, each of them being more or less important for different groups of people. Some of us value fish mostly as a food source, some as a source of livelihood, some for profit and some for their role in ecosystems. This multitude of values creates a trade-off. From one side, we want more food and profit, and this cause overexploitation of many fish species. From the other side, we want to prevent the overfishing and make fisheries more sustainable, either to save fish species for next generations, or to promote healthy ecosystems, or to recover fishing opportunities.

Many institutions worldwide have agreed upon the need for a transition from a single species management of fisheries to an Ecosystem-based fisheries management (EBFM). Such approach recognises that the effects of even the most selective fishery are never limited only to target species but always extend to other species, ecosystem components and habitats. Species do not live in isolation, they interact via predator-prey interactions and competition, which play a central role in the highly interconnected nature of marine ecosystems. EBFM relies on multi-species models to account for these interactions.

Baltic cod, herring and sprat play both a central ecological and economic roles. In the Baltic Sea with a few fish species, herring and sprat are the main fish prey for cod. Lack of alternative prey and predators makes interactions between these three species much stronger. The multi-species model, developed and implemented in this thesis, accounts for interactions between Baltic cod, herring and sprat with reasonable amount of realism (taking the relation between cod and its prey sizes into account and using cod stomach data to verify estimates) and has potential to support EBFM. The model reconstructed number and sizes of cod, herring and sprat during 1974-2013 based on various data collected from fisheries and scientific surveys. In addition, it estimated the number and sizes of herring and sprat that have been eaten by cod and caught by fisheries. I found that smaller cod predate mainly on benthos and larger cod on fish. Cod generally eats smaller sprat and herring than those that are caught by fisheries. However, the overlap in size also exists, meaning that there is some competition between cod and fisheries over herring and sprat.

Multi-species models have their assumptions and uncertainties; however, if different models for same species point in a similar direction, their conclusions are more “trustworthy”. The model described in this thesis was compared with other two similar multi-species models of Baltic cod, herring and sprat to evaluate how fishing intensity should be changed in order to achieve alternative management goals such as, for example, cod recovery, maximising profit of fisheries targeting sprat and herring, or maximising total profits. All models suggested to increase fishing intensity for all three species in order to maximise the profit of fisheries that target herring and sprat. By increasing fishing intensity on herring and sprat fisheries increase the amount of fish they catch and sell. Increasing fishing intensity of cod decreases its number at sea, and as a result less herring and sprat gets eaten by cod and thus become available for fisheries. In the cod population recovery scenario, all models suggested a decrease in cod fishing mortality by at least 20% compared to the levels in 2011-2013.

The model described in this thesis can be used to inform EBFM on how different management scenarios will impact cod, herring and sprat. Furthermore, it may indicate which scenario might secure enough herring and sprat for cod without unnecessary trade-offs from the fisheries side. This may prevent further overfishing of Baltic fishes and make fisheries more sustainable and more profitable in the long run.

Populärvetenskaplig sammanfattning

Marina resurser erbjuder en mångfald av värden för olika grupper av människor. För oss, människor, är fisk födokälla, innebär inkomst och kan generera ekonomisk vinst. Fisk spelar dessutom en central roll i ekosystemet. Denna mångfald av värden skapar potentiella konflikter som kräver avvägningar mellan olika intressen. Å ena sidan vill vi ha mer föda och profit från havet, å andra sidan vill vi förhindra överexploatering av fiskresursen och skapa förutsättningar för ett hållbart fiske. Ett hållbart fiske som återskapar fiskemöjligheter, gör dem långsiktigt tillgängliga för kommande generationer samt bidrar till mer naturliga ekosystem. Många institutioner världen över är eniga om att det kommer att krävas en övergång från enartsförvaltning av fisket till en ekosystembaserad fiskeriförvaltning (EBFF). Angreppsättet utgår ifrån att effekterna av även det mest selektiva fiske aldrig är begränsat till enbart målarten utan alltid har potential att påverka andra arter, ekosystemkomponenter och livsmiljöer. Fiskar kan inte behandlas som isolerade arter utan påverkas av rovdjurs-bytesinteraktioner och konkurrens, processer som spelar en central roll i marina näringsvävar och ekosystem. Ekosystembaserad fiskeriförvaltning kan bland annat få information om dessa interaktioner från flerartsmodeller.

Torsk, sill och skarpsill spelar centrala roller både för fisket och ekosystemen i Östersjön. I Östersjöns artfattiga miljö utgör sill och skarpsill de huvudsakliga födoarterna för större fiskätande torsk. Bristen på alternativa bytes- och rovdjursarter gör länkarna mellan dessa tre arter starka. Flerartsmodellen som konstruerats i denna avhandling tar hänsyn till interaktionen mellan torsk, sill och skarpsill på ett relativt realistiskt sätt och har förutsättningar att kunna stödja EBFF. Modellen rekonstruerade antal och storlekar av torsk, sill och skarpsill under perioden 1974 till 2013 baserat på olika datakällor från fisket och vetenskapliga expeditioner. Dessutom skattas antal och storlekar av sill och skarpsill som torsken ätit och fisket fångat över tid. Min analys av data över vad torsken ätit visade att små torskar främst äter bottenlevande organismer medan större torsk främst äter fisk. Torsken äter framför allt mindre storlekar av sill och skarpsill än de som fångas i fisket. Det finns dock ett överlapp i storlek och därmed förutsättningar för en viss konkurrens mellan torsken och fisket om sill och skarpsill.

Flerartsmodeller inkluderar vissa antaganden och osäkerheter, men i de fall där olika modeller pekar i samma riktning kan resultaten från modellerna anses mer trovärdiga. Modellen som beskrivs i denna avhandling jämfördes med två andra liknande flerartsmodeller innefattande torsk, sill och skarpsill. För modellerna jämfördes hur mängden fiske (fiskeridödligheten) kunde ändras för att uppnå alternativa förvaltningsmål som exempelvis återhämtning av torskbeståndet, maximal vinst i sill och skarpsillsfisket, eller maximal vinst totalt för fisket. Alla tre modellerna indikerade att fiskeridödligheten för alla tre arter borde öka för att öka vinsten i sill och skarpsillsfisket. Genom att fiskeintensiteten efter sill och skarpsill ökar så ökar mängden fisk som kan fångas och säljas. Ett ökat fiske efter torsk leder enligt modellerna till minskad mängd torsk i havet, vilket minskar predationen på sill och skarpsill som därmed i högre utsträckning blir tillgängliga för fisket. I scenariot med återhämtning av torskbeståndet som förvaltningsmål, indikerade modellerna att fiskeridödligheten för torsk behövde minska med minst 20% jämfört med 2011-2013 års nivåer.

Flerartsmodellen som beskrivs i denna avhandling kan användas för att informera en ekosystembaserad fiskeriförvaltning om hur olika scenarier skulle påverka bestånden av torsk, sill och skarpsill. Dessutom kan modellen indikera vilka scenarier som säkerställer att tillräcklig mängd sill och skarpsill finns tillgänglig som föda för torsk, men ändå möjliggör ett fiske på dessa pelagiska arter. En bättre förståelse för interaktionerna mellan fiskarterna och med fiskerierna kan bidra till att minska risken för framtida överfiske och därmed göra fisket mer hållbart och lönsamt på längre sikt.

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